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RESPONSE OF WET MEADOW TUNDRA TO INTERANNUAL AND MANIPULATED TEMPERATURE VARIATION: IMPLICATIONS FOR CLIMATE CHANGE RESEARCH

presented by

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Patricia Gwendolyn Gibbs
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RESPONSE OF WET MEADOW TUNDRA TO INTERANNUAL AND MANIPULATED TEMPERATURE VARIATION: IMPLICATIONS FOR CLIMATE CHANGE RESEARCH

By

Robert D. Hollister

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ABSTRACT

RESPONSE OF WET MEADOW TUNDRA TO
INTERANNUAL AND MANIPULATED TEMPERATURE VARIATION:
IMPLICATIONS FOR CLIMATE CHANGE RESEARCH

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This research is a contribution to the International Tundra Experiment (ITEX). ITEX was established to monitor and make realistic predictions of plant response to climate change. The hypothesis is that short-term warming of ambient temperature will lead to accelerated phenology and increased vigor. Measured characters were date of flowering, number of flowers, stature, number of leaves, and leaf length. Twenty-four small open-top chambers were used to passively warm canopy temperatures in wet meadow tundra at Barrow, Alaska during the summers of 1995 and 1996. Fortuitously the seasonal average temperature difference due to chamber warming and interannual variability were both approximately 1.5 °C; this allowed comparisons of species response to warming caused by the two mechanisms. The statistical significance of species responses to chamber warming and interannual warming were similar 70% of the time. All species showed significant trends of increased vigor or earlier phenologic development under warmer canopy temperatures for at least one character. The most consistent plant response to warmer temperature was increased plant stature.

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Chapter I

INTRODUCTION

I.1 RATIONALE

In recent years there has been considerable interest in species response to elevated temperature and carbon dioxide (CO_2) levels because of concern over anthroprogenically enhanced climate change. Various scenarios of vegetation response to warming have been presented (Bonan *et al.* 1990, Woodward 1993, Monserud *et al.* 1993, Prentice & Sykes 1995, Watson *et al.* 1996, Shugart & Smith 1996). The magnitude of the potential influence climate change could have on the biota was illustrated as early as 1985 by Emanuel *et al.* This model used the Holdridge life zones to delineate current biome boundaries and projected future biome boundaries based on predictions from a global climate model. Although the model was simplistic and, for reasons presented later (section I.2.2-2), likely to be unrealistic, it was useful to exemplify the alarming potential of future climates to modify present ecosystems including the entire elimination of the tundra biome under the future global change scenario.

In all global climate change predictions concerning warming due to atmospheric enrichment of CO_2, the polar latitudes are projected to warm by a larger amount than lower latitudes (Houghton *et al.* 1996). Since polar organisms are adapted to cold climates, it is of interest to ask how well they can adapt to a warmer climate (Stonehouse 1989, McGraw & Fetcher 1992). This project attempts to determine the short-term adjustments in phenology and vigor of plants in a wet meadow tundra at Barrow, Alaska. It is a contribution to a collaborative project known as the International Tundra Experiment (ITEX).

I.2 BACKGROUND

I.2.1 Global Climate Change

Climate has never been and will never be static (MacCracken *et al.* 1990). It is a dynamic and continually changing interconnection of processes operating at many different scales of size, magnitude and time. Throughout the history of the Earth the climate has been changing due to many factors including biotic influence (Budyko *et al.* 1987). The addition of oxygen to the atmosphere during the evolution of photosynthesis greatly influenced many processes on Earth. Even today the biota (primarily soil fauna) emits more CO_2 than humans (Schimel *et al.* 1995). Currently there is considerable emphasis on the potential influence of anthroprogenically increased CO_2 levels in the atmosphere on the Earth's climate and biota. Atmospheric CO_2 levels have been dynamic throughout the Earth's history and these changes show a strong positive correlation with temperature (MacCraken *et al.* 1990).

At the turn of the century, Arrhenius predicted that the amount of CO_2 being emitted by anthroprogenic activity, such as the burning of coal, could result in changes in the Earth's energy balance and likely cause warming (Arrhenius 1896). This assumption was based on the simple knowledge that CO_2 is an absorber of heat energy and is what is now termed a greenhouse gas. Climatologists are currently attempting to model the response of global climate by the use of complex models run on supercomputers, and these equations are fundamentally based on the same basic assumptions of Arrhenius (1896).

I.2.1-1 Global Climate Models

Global Circulation Models (GCMs) are a collection of relatively simple equations attempting to simulate a complex phenomenon (Figure I-2). Most GCMs fundamentally consist of a relatively small number of equations representing the overarching processes occurring in the atmosphere (Henderson-Sellers 1990, Houghton 1997). The models run from half hour to daily time scales on three dimensional atmosphere cells of various sizes that cover the globe (Houghton *et al.* 1996, Figure I-2). The complexity of the models is primarily due the number of iterations run simultaneously for each representative cell and the connectiveness of each cell to its neighboring cells (Figure I-1).

Although the GCMs are not in complete agreement, there are some points upon which nearly all climatologists do agree. Among them, the most relevant to this thesis is that the globe will warm due to anthroprogenic greenhouse gas emissions such as CO_2, methane, and chlorofluorocarbons (CFC's), even in light of all the potential positive and negative feedback processes identified (Houghton *et al.* 1996). Scientists also agree that this warming will not be evenly distributed in time or space (Houghton *et al.* 1990). It is generally agreed that temporal variation of temperature will be greater, causing more extreme weather events and increased variability (Karl *et al.* 1995) and that the high latitudes will warm substantially more than lower latitudes (Weller 1984, Maxwell 1992). GCMs also predict that there will be higher precipitation levels globally and that these levels will be unevenly distributed with greater increases near the coastal and montane regions and lower increases in the centers of the continents. Beyond these predictions, precipitation models are less agreed on than are temperature models (Rizzo & Wiken 1992, Kattenberg *et al.* 1996).

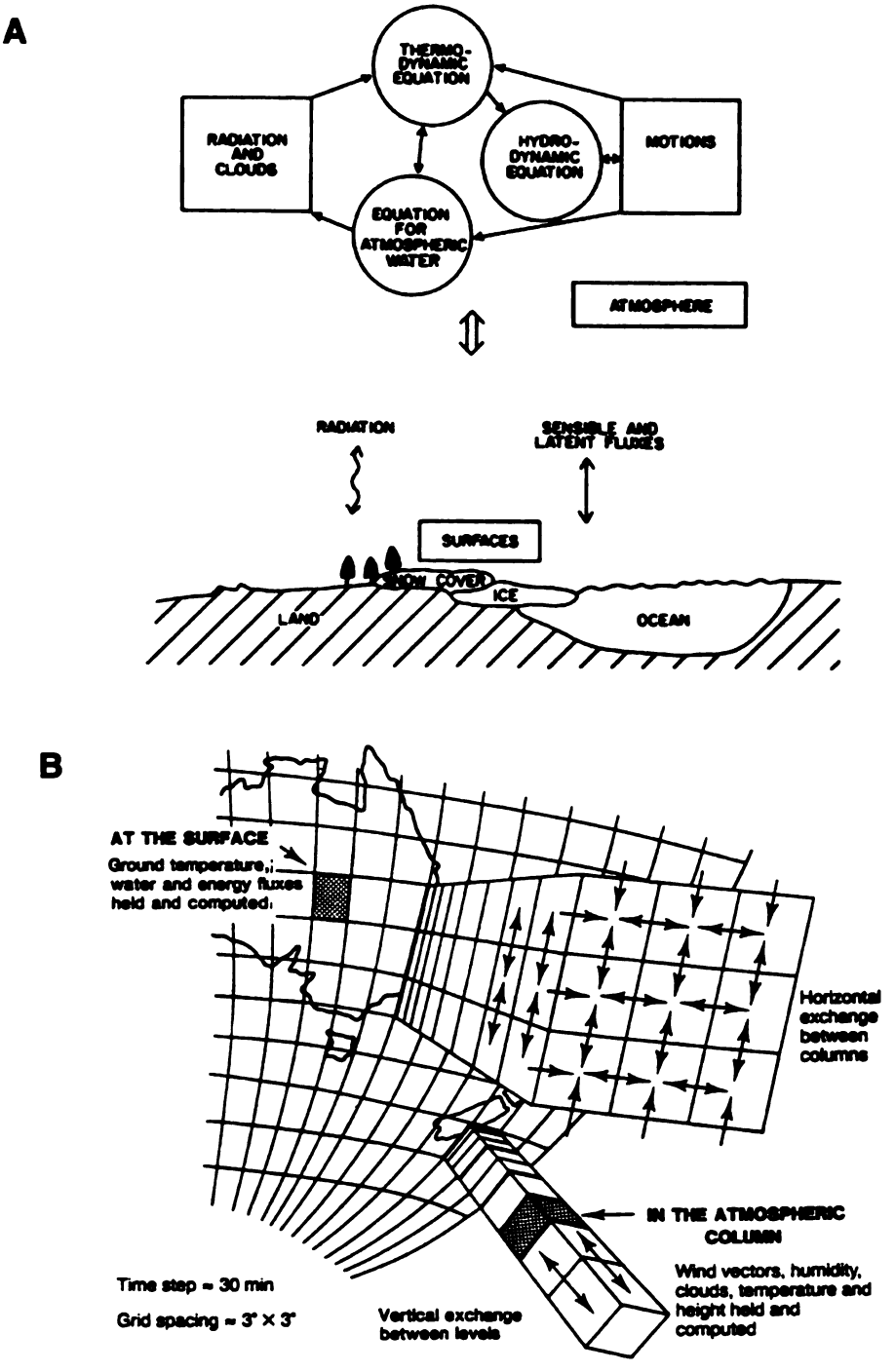

Figure I-1. Conceptual diagrams of a generalized GCM. (A) The basic processes representing equations of a model (Dickson 1986). (B) The scale at which these equations are run (Henderson-Sellers 1990).

I.2.1-2 Current Evidence for Warming

There is evidence that recent global warming is due to anthropogenic activities. The Intergovernmental Panel on Climate Change (Houghton *et al.* 1996) clearly states "the balance of evidence suggests that there is a discernable human influence on global climate." Long-term climatic records show a warming trend over the last century of 1°C. Many researchers have attributed this warming trend to unrepresentative heat islands created by the expansion of the cities from which the long-term data are gathered. Although this may be true in many cases, there are additional independent data sets which also show warming trends; these include oceans surface temperatures (Cane *et al.* 1997), permafrost temperatures (Lachenbruch & Marshall 1986), and glacier retreats (Oerlemans 1994, Dyurgerov & Meier 1997). There is also evidence that the globe is already experiencing increased variations in temperature and precipitation (Hansen *et al.* 1998).

Work by Chapman and Walsh (1993) has shown that high latitudes have warmed more than lower latitudes. They found arctic temperatures have been warming at a rate of 0.75°C per decade, although warming was not uniform around the Arctic and in some areas there was cooling. The Alaskan Arctic is in a region of warming. This warming is attributed to a multitude of factors but the two most important are: positive feedback from decreased albedo due to snow melt; and increased heat flow, because nearly half of the energy in the Arctic is attributed to a flow of heat from lower latitudes (Maxwell 1992).

I.2.2 Vegetation and Climate Change Relations

I.2.2-1 Carbon Dioxide and Plants

Increased carbon dioxide (CO_2) levels can themselves directly affect a plant community. As a plant opens its stomata to obtain CO_2, one of the essential building blocks for photosynthesis, it loses the other, water, *via* the same stomata. This causes a perpetual balance between the need to open the stomata to obtain CO_2 and the need to close them to prevent desiccation. The ratio of water used: sugar synthesized is known as the Water Use Efficiency (WUE). Many physiological processes alter the WUE; it is logically predicted that as atmospheric CO_2 concentrations increase a plant's WUE should also increase. This reasoning has led many to predict that plants will increase their vigor in an atmosphere with increased CO_2 concentrations (Long 1991, Dahlman 1993, Graves & Reavey 1996). This is especially true in crop production when nutrient limitations and competition are potentially minimized. The response of native vegetation and communities is much less predictable because there are many other potential limitations on plant productivity. Furthermore it is expected that species with different physiological adaptations and biochemical pathways will respond differently. For example, C_3 plants are expected to respond more than C_4 plants (Pearcy & Bjorkman 1983).

In a review of studies conducted on natural vegetation, Bazzaz (1990) found that species respond individually to increased CO_2 and that many factors, particularly available nutrients and temperature, affect this response. One of the first and largest community-scale CO_2 enhancement experiments, done on Alaskan Arctic Tundra, found no lasting effects of CO_2 enrichment on the vegetation (Tissue & Oechel 1987, Oechel *et*

al. 1997a). The present consensus is that elevated carbon dioxide levels will have the greatest potential effects on vegetation in water stressed habitats (Chaves & Pereira 1992), and crop (Dahlman 1993) and timber (Eamus & Jarvis 1989) production. Other studies have shown variable long-term effects at the community level (Bazzaz 1990, Culotta 1995, Koch & Mooney 1996). Overall, the conventional wisdom is that CO_2 enrichment alone will have little to no effect in the Arctic (Billings 1995, Oechel *et al.* 1997a).

I.2.2-2 Climate and Plants

Climate has been attributed to be the ultimate and proximate cause of vegetation communities and in turn the animal communities that inhabit them. Many classification schemes use climate as the key to determining vegetation; the most applied of these are the Holdridge (1947) life zone system and the Box (1981) model. These schemes predict vegetation on the basis of variants of precipitation and temperature. When considering the effects of climate on the biota, the range of variability is also of great importance because it is often extreme events that alter a species distribution and ultimately communities (Grime 1990, Sparks & Carey 1995).

Temperature is important for chemical processes and nearly all plants are exotherms, therefore, their metabolic rates are closely dependent on the temperature of their environment. Plants have evolved various physiological adaptations to maintain similar metabolic rates across the latitudinal zones. On a daily basis plants modify internal temperature to various degrees by opening the stomata and altering the angle that they intercept solar radiation. Long-term morphological adaptations allow plants to

change the energy balance between themselves and the environment in order to gain heat or dissipate heat (Bliss 1962). Plants have also evolved similar reaction rates by varying enzyme types and concentrations as temperatures change in order to maintain more constant reaction rates (Christophersen & Larcher 1973, Chapin & Shaver 1985a). These adaptations become more extensive and elaborate in more extreme environments such as the Arctic (Billings 1974, also see section I.2.3-1). In fact, the vegetation of the tundra can be as productive on a daily basis as the vegetation of temperate regions because of adaptations that allow plants to function similarly across a wide range of temperatures (Webber 1978, Bliss 1988). Each species has its own unique suite of adaptations to cope with temperature; therefore, each species has its own ecological temperature optimum and range (Larcher 1975). However, there are limits that higher plants have yet to overcome. These are the cardinal points 0°C and 35°C. Furthermore, the proximate short-term response and the ultimate long-term response of a species to new temperature regimes are not necessarily similar due to their prior adaptive strategies (Chapin 1987, Ozenda & Borel 1989). The combination of these factors and others creates a situation where each species has the potential to respond uniquely to changes in environmental conditions and prediction of a species' new realized niche is a daunting task (Körner 1994, Billings 1997, Huntley & Cramer 1997).

Many researchers predict major changes in species diversity as a result of climate change (Peters & Lovejoy 1992). Fundamentally a population has three potential responses when presented with a change in the environment beyond its tolerance range or ability to acclimate: adapt, migrate, or go extinct (Stonehouse 1989, Holt 1990). Presumably species respond in the above order. Species have the potential to cope with

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new situations and it is likely that in the short-term many species will manage with new climate regimes as they do with interannual variability, although this is dependent on the plasticity of the species. In the long-term species will presumably be out competed by species previously adapted to new climatic conditions (from lower latitudes) before they can evolve new adaptations. In this situation the potential response is to migrate. The classic example of migrations of this type is the progression of species during glacial advance and retreat. However, many species possess low dispersal rates and may not be able to change ranges at the same velocity as the change in climate (Davis 1989, Solomon & Kirilenko 1997). There is also a possibility that analogous high alpine and arctic habitats may no longer exist leaving a species with no place to migrate to. This leaves the final potential response, species that cannot cope or adapt to new conditions or migrate to favorable habitats will become extinct.

The proximate effect of increased temperature will presumably be changes in species fitness. It is believed that temperature is important enough that over the long-term this will lead to an ultimate effect of changes in species distribution. Many cite examples of migration during the ice ages as evidence that species respond to climate, and it was believed that entire vegetation zones moved along with glacial retreat (Oosting 1956). This follows a Clementian view of a climax community where the climate ultimately dictates the community in an orderly way (Clements 1916). Recent more detailed studies show that communities did not move *en bloc*; rather, species responded individually, creating new communities as their individual distributions changed in a Gleasonian way (Gleason 1926, Delcourt & Delcourt 1981, Davis 1989, Bartlein *et al.* 1997). There are many non-climatic factors that species respond to which can modify a

species response to climate; these include nutrient availability, succession, competition, herbivory, and disease to name only a few. Also, species have a migration rate, climatic sensitivity and internal resistance which are predetermined and often confined by prior adaptations and evolutionary history (Löve & Löve 1974, Huntley 1991, Billings 1992, Hoffmann & Parsons 1997). These factors in combination cause species to respond uniquely to climate change. The Emanuel *et al.* model (1985), presented in section I.1, is illustrative of the potential for vegetation change but is fundamentally flawed and limited in its true predictive value because it does not account for the individualistic nature of species responses.

I.2.3 The Arctic System

The nature of the arctic environment creates a situation in which even modest warming has the potential to greatly increase the habitability of the arctic climate because temperatures are habitually close to the biological threshold of 0°C. Figure I-2 graphically depicts the climate of Barrow. From an examination of the figure the potential for the Arctic System to respond to warming can be identified. With modest warming the average daily range of temperatures may no longer overlap zero, snow melt could occur earlier and begin to reaccumulate later, the winter's frozen soil could melt earlier, and the active layer may become thicker. Warming of this layer would increase biological activity. The combination of these factors could create a longer and warmer growing season and increase the availability of nutrients (Kane *et al.* 1991, Anderson 1991, Hobbie 1996, Anisimov *et al.* 1997). Each of these factors alone could effect the system, and there is also the potential for synergism between these factors (Chapin 1984,

Parsons *et al.* 1994). Additionally, the Arctic System is predicted to warm proportionally more than other biomes for reasons presented in section I.2.1-1. Thus, the biota of the Arctic is predicted to respond first and most to climatic warming (Webber & Walker 1991). The combination of these factors makes the Arctic System an important and useful location to study biotic response to climatic change.

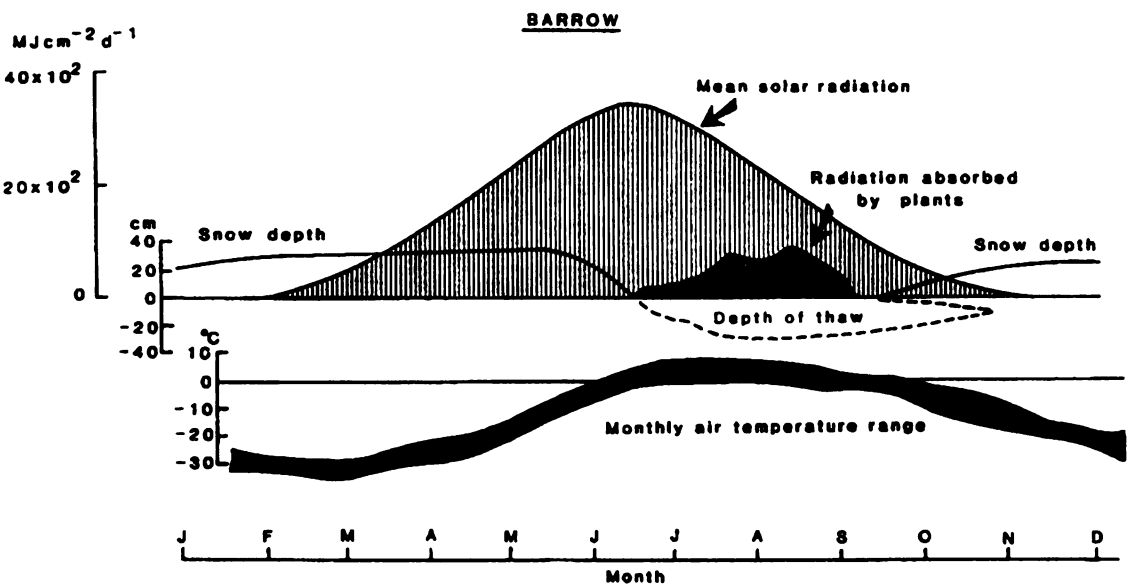


Figure I-2. Diagram of mean, maximum and minimum temperatures, snow depth, active layer thickness, and solar radiation at Barrow (from Chapin and Shaver 1985a).

I.2.3-1 Arctic Plant Adaptations

The arctic environment limits plant growth *via* low temperature, strong winds, low light intensity, low nutrient availability, seasonal water stress, and short growing seasons (Savile 1972, Bliss *et al.* 1973). These constraints reduce carbon gain, thus hindering reproduction and productivity. This is one rationale, among many proposed, for the simple community structure of the tundra system (Warren Wilson 1957, Walker

1995). An equally plausible reason for simple community structure is the relative youth of the tundra biome, which also explains why the flora is of diverse origins and has no endemic genera and relatively few strictly arctic species compared to other biomes (Dunbar 1968).

Tundra plant species often have wide geographic distributions, wide tolerances, and many ecotypes (Billings 1997). Tundra plants are generally long-lived perennials, use asexual and vegetative propagation, allocate large quantities of carbon to reproduction, have large long-lived seed banks, and are polyploid (Johnson 1969, Savile 1972, Molau 1993a). These attributes are considered to be useful adaptations to life in the tundra environment. The life form spectrum for the tundra is termed chamaephytic. The spectrum is generally composed of 0% phanerophytes, 23% chameophytes, 61% hemicryptophytes, 15% cryptophytes, and less than 1% therophytes (Oosting 1956). arctic species often fall into four groups based on their distribution: hyperarctic (inhabit the high arctic), eurarctic (inhabit the entire arctic), hemiarctic (inhabit the mid arctic, not the extremes of high or low), and hyparctic (inhabit the low arctic and taiga) (Chernov 1985). These groupings overlap considerably with the groupings of characteristic species within Young's zones, which are based on climate and species composition (Young 1971). High arctic communities and species have been shown to respond more to temperature manipulation than low arctic communities and species (Wookey *et al.* 1993).

Many arctic plants have evolved ways to absorb heat and maintain considerably higher tissue temperatures than their local environment. Some of these morphological adaptations are, short stature, maintaining dead parts to reduce wind, and dark pigmentation (Savile 1972, Mølgaard 1982). In order to compensate for low rates of

metabolic and physiological process at low temperatures Arctic plants have evolved high enzyme concentrations which enable them to maximize metabolic and physiological processes including photosynthesis, nutrient absorption, and growth at temperatures far lower than related temperate species (Larcher 1975, Heide 1983, Chapin & Shaver 1985b). Due to morphological and physiological adaptations, arctic species are generally believed to be more limited by indirect effects of temperature on other abiotic factors namely nutrient availability and length of growing season than direct temperature effects on plant physiology (Chapin 1984, Chapin & Shaver 1985a).

The low level of plant nutrients in arctic environments is generally believed to be due to slow decomposition and turnover (Swift *et al.* 1979, Hobbie 1996). Low soil fertility is verified by many fertilization experiments and is supported by the dominance of species with high root to shoot ratios (Babb & Whitfield 1977, Shaver & Chapin 1986, Henry *et al.* 1986, Jonasson 1992). The problem of low nutrients is compounded by the fact that tundra plants have higher than average nutrient demands due to their high enzyme and lipid concentrations (Chapin & Shaver 1985a). In situations where nutrients and water are not limiting, the largest constraint on productivity is the length of the growing season. On a daily basis, the relative growth rate (RGR) of *Eriophorum angustifolium* of 128 mg g^{-1} d^{-1} is greater than the range for temperate plants where RGR levels range from 16 to 60 mg g^{-1} d^{-1} (Chapin & Shaver 1985a). Tundra plants are often evergreen or semi-evergreen (often referred to as wintergreen), and often preform vegetative and flowering buds up to several years in advance (Sørensen 1941). This may be an adaptation to the short growing season. A further adaptation my be the general lack protective scales or hard parts over buds so that they can readily expand at the onset of

snowmelt and begin to grow while their roots are still frozen (Savile 1972, Shaver & Kummerow 1992).

Two often distinctly different growth strategies have been recognized in the Arctic. These are known as periodic and aperiodic growth (Sørensen 1941). Species that show periodic growth are considered to be less receptive to changes in heat accumulation and to generally grow to a predetermined size regardless of a current season's climate. Species that show aperiodic growth commonly respond directly to climate and may thus be thought to take advantage of warmer and especially late season temperatures. Aperiodic growth may allow a species to fully utilize the growth potential of a season; however, the individual could be more susceptible to harsh summer conditions and winter injury (Sørensen 1941, Savile 1972). The periodic growth strategy may be considered to be more conservative and to reduce the risk of damage due to harsh weather. Periodic growth is more common in the Arctic (Savile 1972).

I.2.3-2 Barrow Alaska

Barrow was chosen as the field site location because it has cold summers, a long climatic record, site management and protection, and an ecological database (Shaver 1996). The vegetation of the area has been well described by many including Britton (1957), Cantlon (1961), and Webber (1978). It was the site for the Tundra Biome program of the International Biological Programme (Brown *et al.* 1980). Barrow has been the home of the Naval Arctic Research Laboratory (NARL) and its succeeding institutions since 1947 and has one of the longest and richest histories of research of any location in the Arctic making it one of the best known ecosystems of any in the world

(Reed & Ronhovde 1971). A Climate Diagnostic Laboratory run by NOAA is located within 3 km of the site and provides historical climate data as well as detailed current conditions and is the site of one of the longest CO_2 and greenhouse gas records in the world (Hofmann *et al.* 1996). Recently the community of Barrow established the Barrow Environmental Observatory (BEO) to preserve a large tract of tundra for future research. Thus, because of its huge potential to respond to modest warming, its inherent simplicity, and its historical record, Barrow serves as an ideal location to study species response to climatic change.

I.3 Research Framework

The results presented in this thesis are a subset of two distinct yet interacting research programs, Arctic Systems Science (ARCSS) and the International Tundra Experiment (ITEX). All work for the thesis was completed as a part of the Arctic Ecology Lab (AEL) on Michigan State University. The logos of these 3 research groups are presented in Figure I-3.

I.3.1 Arctic System Science

The Arctic System Science (ARCSS) Program is a subprogram of Polar Programs within the National Science Foundation (ARCUS 1993). ARCSS takes a whole-system approach to understanding the response of the Arctic System to global change and is particularly concerned with the mechanisms and consequences of the amplified response of the high latitudes to greenhouse warming. A principal goal of ARCSS is to enable the

prediction of the future state of the Arctic System, on seasonal to century time scales, by integrating observations, process research, modeling and assessment. This ITEX project is most closely connected to the Land / Atmosphere / Ice Interactions (LAII) component of ARCSS. The response of tundra vegetation to warming documented in this thesis will ultimately be incorporated into models that attempt to predict vegetation response to global change.

I.3.2 The Arctic Ecology Lab

The Arctic Ecology Lab (AEL) is housed in North Kedzie Hall on the Michigan State University (MSU) Campus. MSU is a large, well-equipped research university with superior library, computational, and soil / stable isotope analyses facilities. The knowledge resource at MSU is extensive and includes an interactive network of 83 Ecology and Evolutionary Biology faculty members representing 12 college departments from Anthropology to Zoology. The AEL occupies five offices and houses 1 faculty member, 2-3 graduate students, and 3-7 undergraduate assistants. Each office has its own phone, computer, and printer. The computer facilities were designed for graphics and statistical analyses and include a scanner and color laser printer. All equipment is connected to the web and locally networked. The AEL is an active collaborator with the Computational Ecology and Bioinformatics Laboratory (CEBL). CEBL is designed to provide computational facility to conduct spatial analysis research and use intensive mathematical models to address global and complex systems analysis. The AEL library contains over 15,000 volumes and 30,000 reprint with emphases in Cold Regions Ecology, Global Change, and Botany; it also houses an extensive map and aerial

photograph collection of the Northern Alaska, particularly the Barrow area and the National Petroleum Reserve.

I.3.3 The International Tundra Experiment

The International Tundra Experiment (ITEX) is a collaborative effort involving scientists from 11 countries including all the Arctic Nations (Figure I-4). ITEX seeks to examine the response of circumpolar cold adapted plant species to environmental change, specifically to an increase in summer temperature. Empirical knowledge based on experiments coupled with available evolutionary history, ecology, and genetics was chosen as the best way to predict species response to climate change. The ITEX research model combines long-term and short-term experimentation with monitoring and has the elegance and simplicity called for to understand ecosystem response and vulnerability to change (Tilman 1987, Rastetter 1996). The experiment is designed to examine the effects of temperature change; maximize geographic representation, by minimizing technical and equipment requirements; be long-term; focus primarily on species; and, if resources permit, allow for genetic and system level studies (Molau & Mølgaard 1996). Participation may be at several levels of complexity and sophistication depending on interests and available funding support. Each ITEX site operates the base experiment, which uses small open-top green houses to warm the tundra. These passive chambers effect plant growth and phenology in a variety of ways (Marion *et al.* 1997, Henry & Molau 1997). Collectively the ITEX network is able to pool its data sets to examine vegetation response at varying levels, for example genetics (from ecotype to functional type), across space (from habitats to ecosystems) and over time (Walker 1996a).

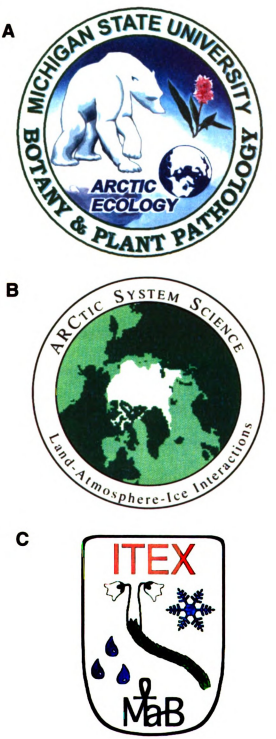


Figure I-3. Logos of the research efforts with which this project is networked: (A) the Arctic Ecology Lab, (B) Arctic System Science and (B) the International Tundra Experiment.

I.3.3-1 The Network and its History

In 1990 global warming research focused on responses and roles of the abiotic factors of ice, atmosphere and ocean in the Arctic System or on broad ecosystem functions. By doing so, the research omitted organism specific responses to predicted warming (Webber 1990). Without this later information it is impossible to predict the composition of future biotic communities and living resources. Therefore, a workshop was held to explore the development of an international, Arctic-wide network of observations and experiments to look specifically at the response of tundra plants to climate warming. The workshop involved 50 scientists from many nations and resulted in a project and an experimental protocol (Webber & Walker 1991, Molau 1993b). The first official ITEX measurements were made in 1992 and now the network comprises 26 sites. ITEX is coordinated from the Danish Polar Center, Copenhagen. U.S. ITEX projects are part of the NSF Arctic System Science (ARCSS) Program of the U.S. Global Change Research Program. ITEX scientists meet annually to share experiences and coordinate efforts. They met in 1996 at the National Center for Ecological Synthesis, Santa Barbara (NCEAS), CA where they used meta-analysis in an innovative way to integrate pooled data sets (Gurevitch & Hedges 1993). ITEX will continue this approach to synthesis as the data set grows. ITEX scientists are publishing in the open literature, including a special issue of Global Change Biology (Henry & Molau 1997). The ITEX *modus operandi* for studying biotic response to climatic variation is well regarded and is used as a model for other studies. For example, the Circumpolar Active Layer Monitoring program (CALM) has modeled their coordinated effort after ITEX (Brown 1997).

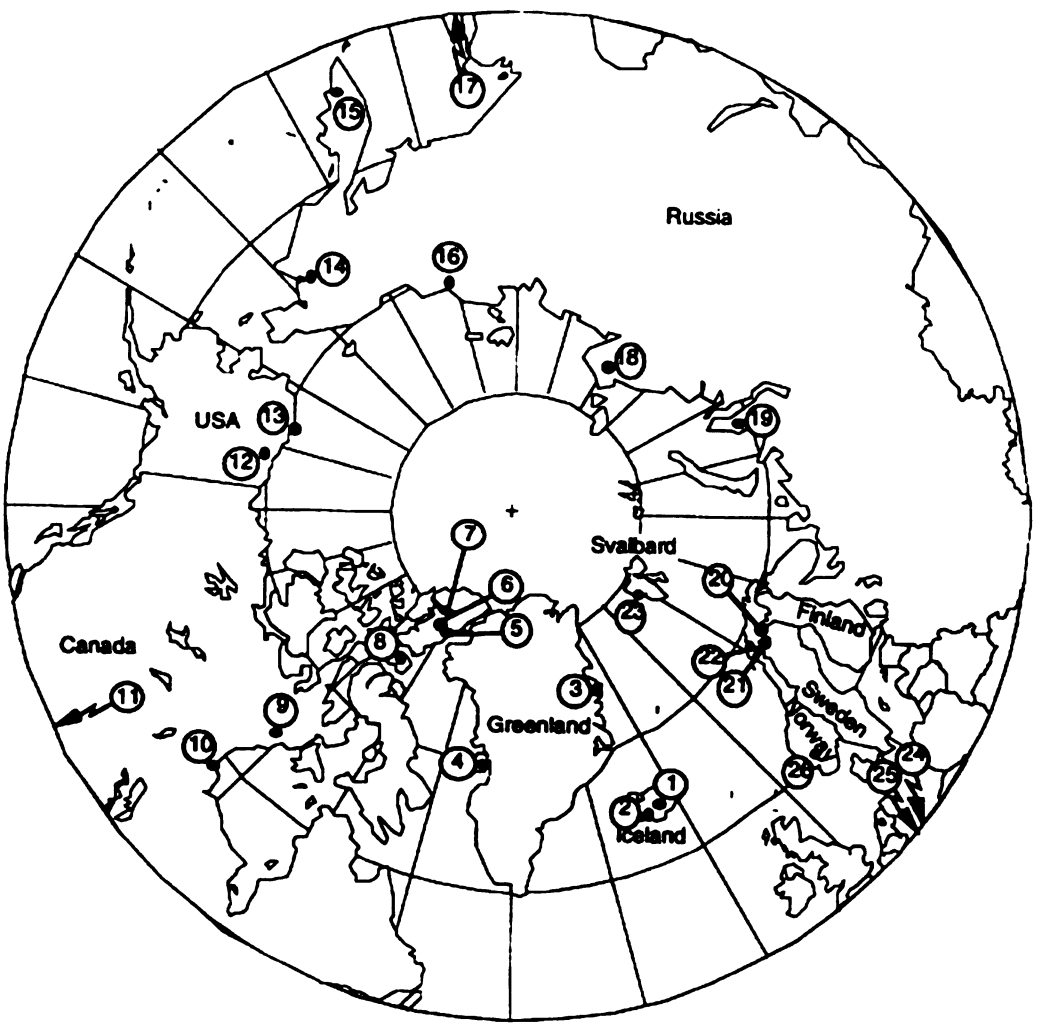


Figure I-4. Map of the ITEX field sites. Site 13 is Barrow (Molau & Molgaard 1996).

I.3.3-2 The Chamber

A passive open-top chamber was chosen as the preferred method to warm the tundra because of its low cost, its ease of replication, and freedom from the need of mechanical investment or power supply (Figure I-5). An open-top was chosen to lower temperature extremes and allow more direct solar radiation, more natural levels of humidity and gases such as CO_2, direct entry of precipitation, and easier access of pollinators and herbivores. The structural soundness of the chambers enables them to hold up to the rigorous of the arctic climate and be used for many years. Due to justified concerns about the use of chambers (Kennedy 1995), an extensive documentation of chamber performance was done and is presented in Chapter III.

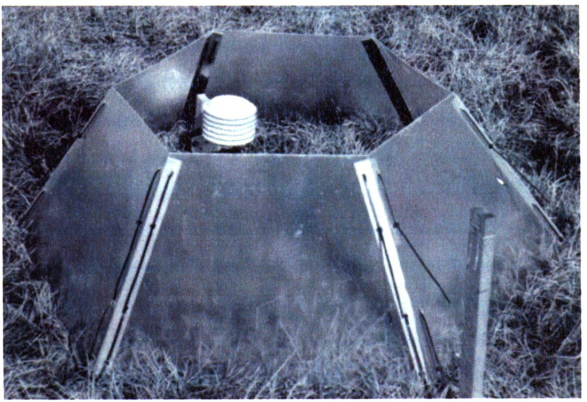


Figure I-5. An open-top chamber (OTC).

I.4 QUESTIONS AND HYPOTHESES

For clarity, the responses of plants to temperature are discussed under three themes: phenology, plant vigor, and species patterns. Each of these themes are discussed separately in terms of underlying questions, specific hypotheses, and the rationale.

I.4.1 Phenology Response

Question: In what way and to what extent will the phenology of selected plants respond to variations of growing season temperature and increased canopy temperature?

Hypothesis 1a: Flowering will occur earlier under warmer conditions.

Hypothesis 1b: Flowering will occur at approximately the same degree day threshold.

Rationale: Species in sheltered depressions and on the south facing slopes flower earlier than individuals in the adjacent environment due to warmer microclimates (Sørensen 1941, Bliss 1962, Savile 1972). Observations along climatic gradients also show that a species flowers earlier at the warm ends of its climatic range (Sørensen 1941, Walker & Webber 1979, Shaver *et al.* 1986). Although arctic plants have adapted to low temperature, their tissue temperatures are generally below their optima for most physiological processes (Chapin & Shaver 1985a). Temperature is believed to be critical to growth and development and degree day accumulations have been shown to be strongly correlated with onset of phenological events (Lieth 1974, Wielgolaski & Karenlampi 1975, Shaver & Kummerow 1992). Therefore we would expect species to respond to warmer microclimates and warmer field seasons with earlier onset of

phenologic events, namely flowering (Dennis 1969, Walker *et al.* 1995, Mølgaard & Christensen 1997, Walker 1997).

I.4.2 Vigor Response

Question: By how much and in what way will the vigor of selected plants respond to variations of growing season temperature and increased canopy temperature?

Hypothesis 2a: Plants will produce more flowers under warmer conditions.

Hypothesis 2b: The height of inflorescence will be taller under warmer conditions.

Hypothesis 2c: The length of leaves will be longer under warmer conditions.

Rationale: Although arctic plants are generally believed to be acclimated to lower temperatures, their optima are above most prevailing tissue temperatures. Therefore, we would expect greater carbon accumulation and overall vigor of a plant with increased temperatures (Chapin & Shaver 1985a). Sexual reproduction is only occasional successful in the arctic environment, but is believed to be important. If a plant has additional photosynthate, it may be allocated to reproduction and consequently flower more (Bliss 1988, Molau 1993a, Jonsdottir 1995). Arctic plants are generally short in stature and live near the ground's surface where one might reason that biotemperatures can be maximized (Warren Wilson 1957, Hansen 1973, Bliss 1988). Nevertheless, there is an advantage to increasing the length of the inflorescence above the plant canopy to enhance dispersal potential (Savile 1972). With warmer air temperatures plants are predicted to increase in stature. The leaf length is also predicted to increase because of increased overall health of the plant, and the potential for greater light competition (Walker 1986, Callaghan *et al.* 1989, Chapin *et al.* 1995, Harte & Shaw 1995).

Additionally, specimens are generally taller and have longer leaves in their warmer ranges or microclimates (Sørensen 1941, Dennis 1968, Körner & Larcher 1988).

I.4.3 Species Patterns of Response

Question: Are there species responses to temperature that can be generalized or do all species respond uniquely?

Hypothesis 3a: Short-term plant phenologic response to canopy warming will mirror responses of the controls observed in warm years.

Hypothesis 3b: Short-term response of plant vigor observed in the chambers will mirror responses of controls observed in warm years.

Hypothesis 4: Plant species will respond individualistically to temperature.

Rationale: Every species has evolved its own way to cope with the climate and each has approached the problem from very diverse historical origins (Savile 1972, Billings 1992). Studies have shown that arctic species respond to external stimuli individually (Chapin & Shaver 1985b, Oberbauer *et al.* 1986). Therefore, it is predicted that species will also respond uniquely to warming.

The results of hypotheses 3a and 3b will determine the efficacy of the chambers as a temperature enhancement device in terms of plant response. If the chambers main effect is to raise temperature, then the species' short-term response to chambers should be similar to a species' interannual variability in flowering. If changes in vigor are strongly related to temperature and the chambers do not produce undesirable secondary effects, then short-term response to warming due to chambers should mirror the response due to interannual variability in seasonal temperature.

Chapter II

METHODS

II.1 STUDY AREA

The research area is located within the Barrow Environmental Observatory (BEO) approximately 8 km north the village of Barrow, Alaska on the Barrow peninsula (71°18'N, 156°40'W)(Figure II-1). The BEO is a protected tundra landscape covering 15 square kilometers owned by the Ukpeaġvik Iñupiat Corporation (UIC) which is leased to and managed by the Barrow Arctic Science Consortium (BASC). The Barrow Region has a long and rich research history (see section I.2.3-2). The field site is located within an Arctic System Science (ARCSS) grid and within 100m of an ITEX site in a dry heath community (Figure II-2, Bay 1995,1996, Walker 1997). There are several ARCSS grids throughout the Arctic that monitor long-term change in variables such as snow depth, active layer progression, and plant community composition (Brown 1997).

The Barrow Peninsula is a spit of land surrounded by the Chukchi sea on the west, Elson Lagoon on the east, and the Arctic Ocean to the north. The Peninsula is roughly 25,000 years old (Brown & Sellmann 1973). The coastal tundra in this region is dominated by a pattern of ice wedge polygons, and shallow lakes. The research area is contained within a wet meadow community situated on the north eastern end of Central Marsh in a transition zone between the marsh proper and a former raised beach ridge surrounding the marsh on the north side (Figure II-2). The elevation of the site above mean sea level is 3 ± 0.5 m and has a fine silt substrate and histic pergelic cryaquept soils with very poor drainage (J. Bockheim, personal communication). The field site is on a recovered former vehicle track that ran along the edge of Central Marsh.

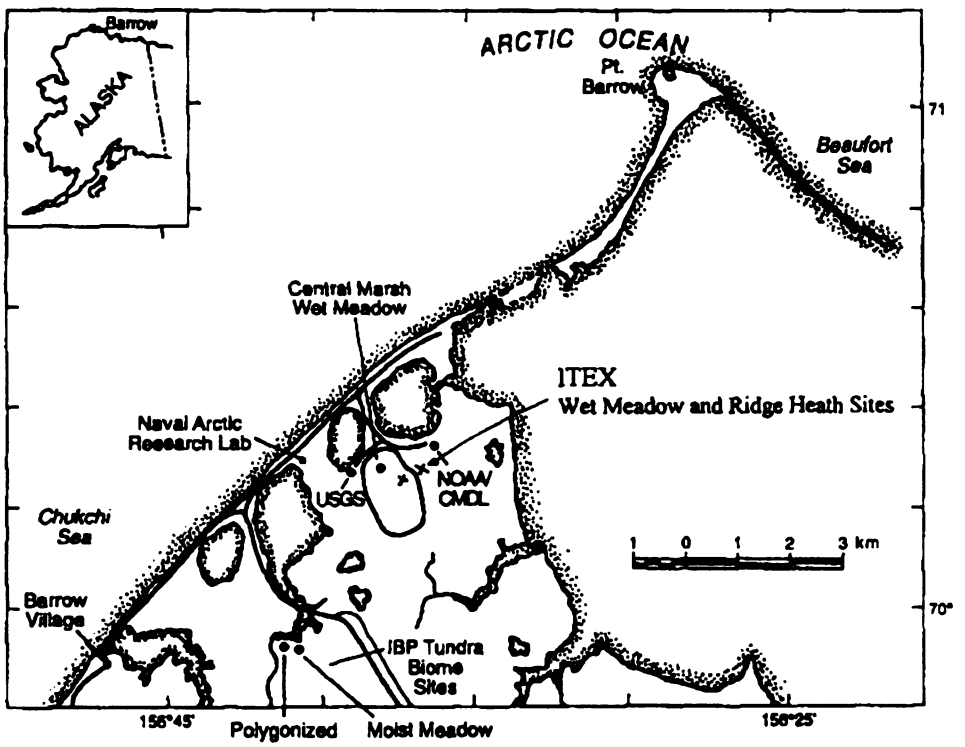


Figure II-1. Map of Alaska and the Barrow Peninsula showing the ITEX field sites and other historical research locations.

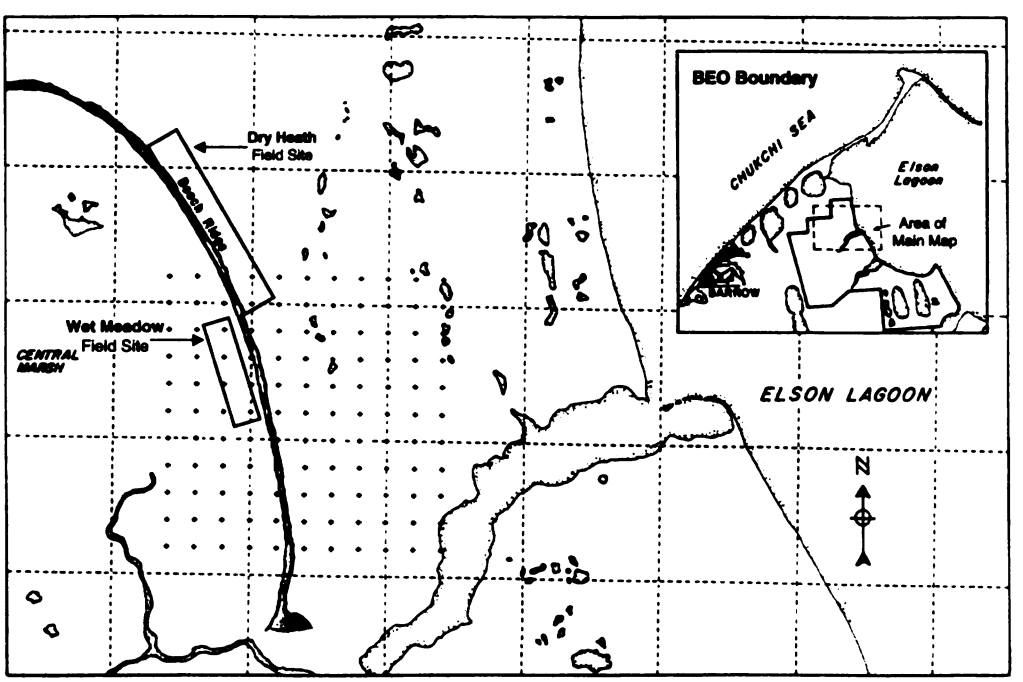


Figure II-2. Map of the research area, showing the ARCSS 1x1km grid (crosses), the field sites, beach ridge, and other prominent features. The Boundary of the Barrow Environmental Observatory (BEO) is shown on inset (Hinkel *et al.* 1996).

The climate of Barrow consists of long cold winters and short cool summers during which the temperature can fall below zero on any day (Table II-1, Figure I-3). The sun does not rise from November 18 to January 24 and rise is 24 hours a day from May 10 to August 2. The snow free period is variable but generally begins in early June and continues until early September during which time an average of 251 degree days are accrued (Brown *et al.*1980). The summers are generally cloudy, foggy and wet with a summer average of over 80% humidity during which 37% of the annual precipitation is received (Brown *et al.* 1980).

Table II-1. Climate data for the Barrow region (Brown *et al.* 1980).

	Temp (°C)	Precip (mm)	Windspeed ($m\ s^{-1}$)	Solar radiation ($MJ\ m^{-2}\ day^{-1}$)	Day Length (hr)
Jan	-25.9	5.8	5.0	0.0	0.7
Feb	-28.1	5.1	4.9	1.6	6.8
Mar	-26.2	4.8	5.0	7.4	11.7
Apr	-18.3	5.3	5.2	15.5	16.7
May	-7.2	4.3	5.2	21.9	23.1
June	0.6	8.9	5.1	23.0	24.0
July	3.7	22.4	5.2	18.5	24.0
Aug	3.1	26.4	5.5	10.8	19.0
Sept	-0.9	14.7	5.9	5.0	13.4
Oct	-9.3	14.0	6.0	1.7	8.6
Nov	-18.1	7.6	5.6	0.2	2.4
Dec	-24.6	4.8	5.0	0.0	0.0
Year	-12.6	124.1	5.3		

The vegetation of the region is coastal tundra dominated by graminoids, most notably *Carex stans* and *Eriophorum* species. The Barrow tundra is acidic and contains a major bryophyte component and an abundance of lichens. Several relatively distinct vegetation associations are present in the region including: *Luzula* heath, *Salix* heath, *Carex-Poa* meadow, *Carex-Oncophorus* meadow, *Dupontia* meadow, *Carex-Eriophorum* meadow, *Arctophila* pond margin, and *Cochlearia* meadow (Brown *et al.* 1980). The location of the field site is within a *Carex-Eriophorum* meadow. The species

composition determined by the point frame method (Walker 1996b) is given in Table II-2 for the combined experimental open-top chamber plots and control plots in the site.

Table II-2. Species composition of the field plots.

VASCULAR PLANTS	Percent Cover	VASCULAR PLANTS	Percent Cover
Carex stans	40.50	*Cochlearia officinalis*	0.41
Eriophorum triste	13.51	*Salix rotundifolia*	0.38
Duptonia fisheri	10.97	*Draba lactea*	0.37
Stellaria laeta	5.75	*Petasites frigidus*	0.37
Saxifraga hirculus	5.55	*Ranunculus nivalis*	0.08
Eriophorum russeolum	3.47	*Ranunculus pygmaeus*	0.05
Cerastium beringianum	3.06	*Alopecurus alpinus*	0.04
Saxifraga cernua	3.06	*Draba micropetala*	0.04
Cardamine pratensis	2.55	*Arctophila fulva*	0.03
Carex subspathacea	1.58	*Eriophorum scheuchzeri*	0.03
Hierochloe pauciflora	1.49	*Salix pulchra*	0.01
Saxifraga foliolosa	1.30	*Saxifraga caespitosa*	0.00
Saxifraga hieracifolia	1.24		
Poa arctica	1.22	LITTER	25.50
Juncus biglumis	0.74	BRYOPHYTE	43.20
Calamagrostis holmii	0.64	LICHEN	2.20
Luzula arctica	0.61	ALGA & MUSHROOM	0.30
Luzula confusa	0.46	BARE GROUND	0.10
Stellaria humifusa	0.46		

II.1.1 Site Establishment

The data presented in this thesis were recorded during the field seasons of 1995 and 1996. The field site was established on June 25, 1995 along a snow bed on the northeastern side of Central Marsh. Areas of high plant species diversity containing preferred species were chosen for plot establishment. Twenty-four controls and 24 experimental designations were determined randomly from the predetermined plots. The plots were located 1-6 m from the retreating snow bed and formed a near linear pattern due to the nature of the snow bed (Figure II-3). The plots were chosen as close to one another as was possible to minimize variation in elevation, hydrology, soils, and plant community composition. The site spans a length of less than 300 meters (Figure II-4). Chambers were installed on the day of site establishment. Control plots were marked by

using wooden stakes and string to deliminate a 1x1m square of tundra. A wooden stake was installed near each chamber for identification purposes. Metal tags were used to mark each plot in addition to using waterproof markers. A path was established along the south edge of the plots to minimize disturbance due to foot traffic.

Chambers were removed on August 22, 1995 to avoid damage from local snowmobiles and to avoid unnatural build up of snow in the chambers. They were reinstalled between June 4 and 14, 1996 (the day after an individual plot became completely snow free) and removed on August 21, 1996.

Figure II-3. The field site shortly after establishment in 1995 (courtesy of Christian Bay).

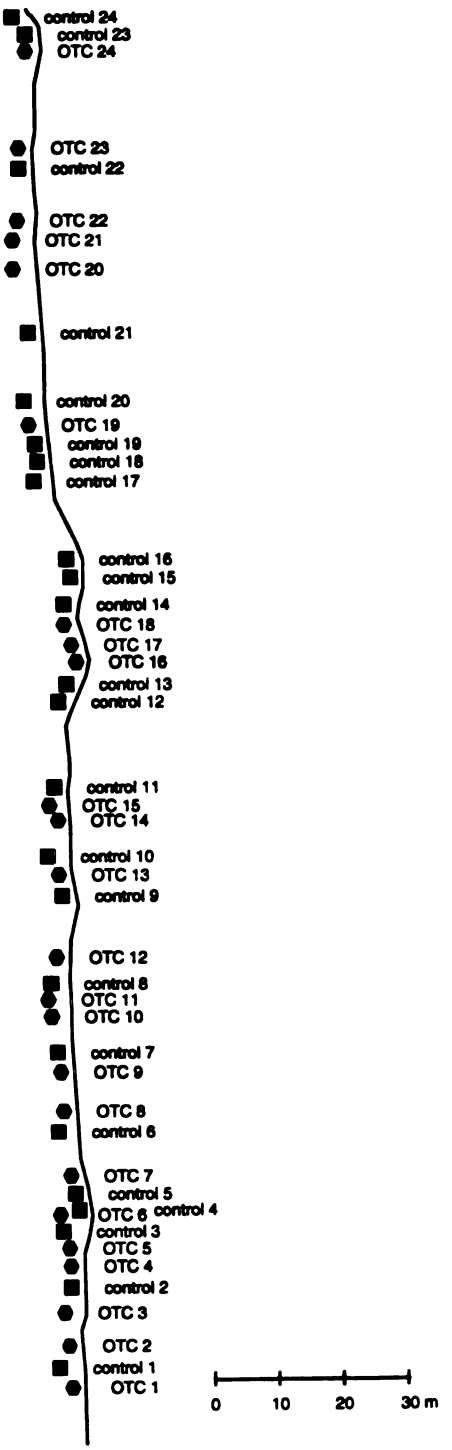


Figure II-4. Map of field site showing each plot.

II.2 Abiotic Documentation & Chamber Performance

II.2.1 Chamber Design

The open-top chambers (OTC's) are hexagonal with sloping sides constructed of Sun-Lite HP™ fiberglass (Solar Components Corporation, Manchester, NH). This material is commonly used in many horticultural settings due to its high solar transmittance in the visible wavelengths (86%) and low transmittance in the infra-red range (<5%) (Molau & Mølgaard 1996). The height of the chamber is 35cm and the distance between the parallel sides is 103cm at the base and 60cm at the top (Figure II-5). The open-top reduces shading effects and allows ventilation and access by pollinators. Marion *et al.* (1993 & 1997) documented the general performance of the ITEX OTCs and a detailed documentation of the chamber performance at Barrow is given in Chapter III.

II.2.2 Climate Monitoring

II.2.2-1 Macroclimate Monitoring

The macroclimate data for Barrow, Alaska were obtained from the National Ocean and Atmospheric Association's (NOAA) nearby climate station. The station is staffed year round and collects general climate data as well as several trace gas concentrations (Stone *et al.* 1996).

II.2.2-2 Microclimate Monitoring

Both Hobo® and StowAway™ data loggers manufactured by Onset Inc. (Appendix Figures A-1 - A-5) collected temperature and relative humidity data within chambers and over control plots during the snow free season only. The StowAway™

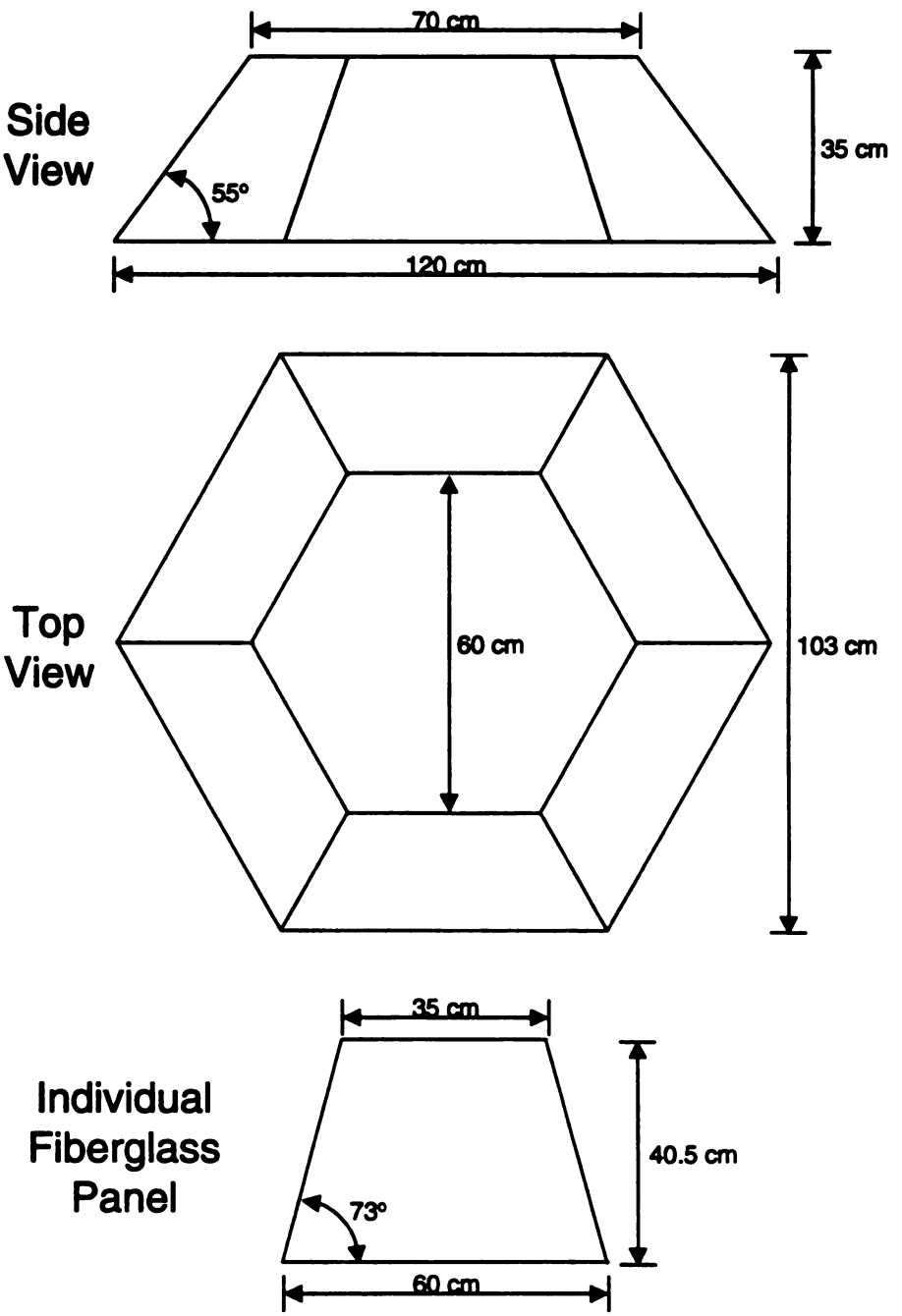


Figure II-5. The design of the open-top chambers.

data loggers are an expanded version of a Hobo® data logger that includes more memory and a more frequent recording interval. Data loggers were set to record every 12 to 80 minutes depending on the sensor type from the date of plot establishment until August 18. The placement of temperature data loggers was determined randomly each year; relative humidity logger placement was determined randomly from the plots already containing temperature loggers. Loggers or sensors were housed in "gill six plate" thermistor shields at approximately 13cm above the ground in the most northerly corner of the chamber (see Figure II-6A).

II.2.2-2.1 Horizontal and Vertical Temperature Distribution

A secondary monitoring program was established near the field site to collect more detailed data on the horizontal and vertical distribution of warming within the chambers. The horizontal distribution of warming within the chamber was established by placing two arrays of thermistors at 1cm above soil surface within two chambers and four thermistors nearby outside the chambers as the controls. The spacing for both arrays was a thermistor at: approximately 10cm from the north edge of the chamber, half way between the north edge thermistor and the center, the center, half way between the center and the south edge thermistor, and approximately 10cm from the south edge (Figure II-6). For the vertical distribution of warming there were no replicates due to a limited availability of sensors. In the one chamber and the nearby control, the spacing of the sensors was: 1, 6, 11, 16, 21, 26, 31, and 36cm above the soil surface (Figure II-6). All sensors were operated at a recording interval of 9 minutes from June 20 to July 28, 1996

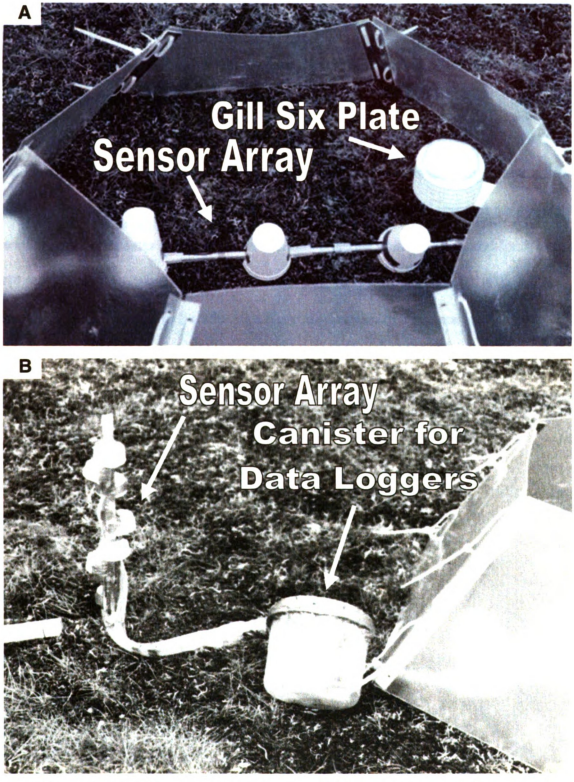


Figure II-6. The spatial arrangement of temperature probes: (A) horizontal distribution and (B) vertical distribution.

for both the horizontal and vertical sampling. Sensors were shielded from direct sunlight with shelters made from inverted polystyrene foam drinking cups (Figure II-6).

II.2.2-2.2 Light Distribution

The distribution of light entering the chamber was monitored with StowAway™ light sensors (Appendix Figure A-5). Four sensors were placed within one chamber. Two sensors were placed within the center of the chamber and one approximately half way between the center sensors and the chamber edge for both the north and south edges (Figure II-7). Two sensors were placed outside the chambers as controls. All sensors were run from August 1 to 21, 1996 at a recording interval of 5 minutes.

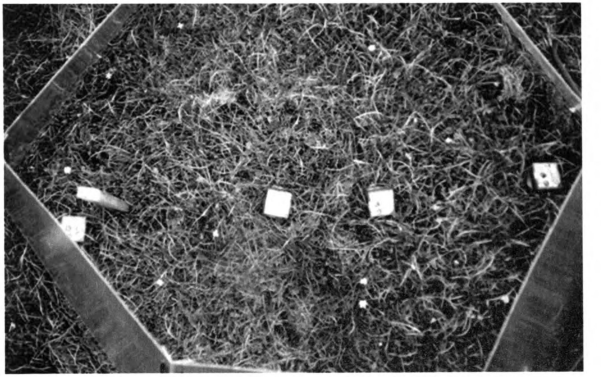


Figure II-7. The placement of four light sensors within a chamber.

II.2.3 Below Ground Monitoring

II.2.3-1 Soil Temperature

Soil temperature was monitored with the use of both Hobo® and StowAway™ data loggers with sensors placed in the ground at a spacing of 1, 5, 10, and 15cm beneath the surface (Figure II-8). The loggers were in operation from July 10 to August 18, 1996 at a 16 minute recording interval. The same sampling protocol was used to monitor the soil temperature from an ITEX field site in a dry heath community within 100 m of the wet meadow field site (Walker 1997).

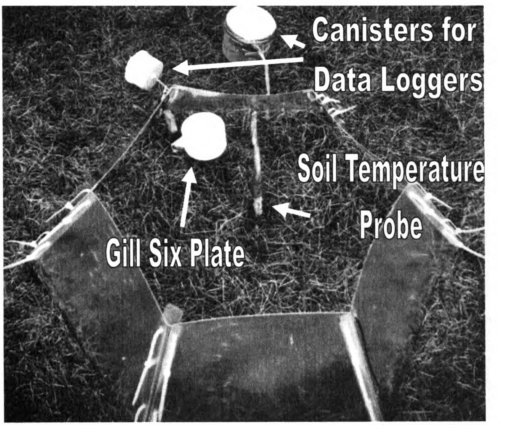


Figure II-8. The chamber within which soil temperature monitoring was conducted.

II.3.3-2 Active Layer Monitoring

The active layer thickness was measured to the nearest cm by thrusting a small metal rod into the ground surface until frozen ground was reached (Figure II-9). The active layer thickness was recorded daily at the beginning of the thaw season. For the remainder of the field season measurements were made weekly in 1995 and every 10 days in 1996. The active layer thickness for each plot was determined by probing outside the control plot within 30cm of the four corners or by probing the center of the plot in OTCs. Previous holes were not used for later probings because of the potential for unrepresentative depths of thaw caused by heat sinks from water percolation and air movement within the former holes (Hinkel *et al.* 1997).

Figure II-9. Probing the active layer.

II.2.4 Degree Day Calculation

In this thesis, degree days and thawing degree days are used synonymously. The traditional growing degree days based on 5°C was not used because in Barrow 0°C is generally the cardinal temperature at which growth begins (Dennis *et al.* 1978). In temperate or tropical sub tropical regions the cardinal temperatures are generally 5°C or 10°C respectively. In order to avoid confusion the term thawing degree days is used rather than growing degree days.

Thawing degree day accumulation from snow melt (TDD*) was calculated by using the temperature data collected (between 12 and 80 minute intervals depending on instrumentation). Plots were established after snow melt in 1995, therefore degree day accumulations from snow melt until plot establishment were estimated by calculating the thawing degree day accumulation from standard NOAA screen temperature data. This estimate was necessary because the site was established after the estimated snow melt date of June 19th. The estimated TDD* is likely within five degree days of the true number. August 18 was chosen as an ending date for meaningful degree day accumulation. This is based on the observation that nearly all Barrow species begin dormancy or senescence in mid August (personal observation, Miller *et al.* 1980). Also, August 18 was within a week of when the end of season plant measures, described in the next section, were collected both years.

II.3 VASCULAR PLANT MONITORING

Individuals of each species present were permanently tagged in each plot. In 1995 galvanized nails were used to mark the individuals; the nails were later replaced with wooden sticks in 1996 because they were deemed easier to use and less likely to alter the canopy thermal regime. The first three individuals of a species to turn green within a plot were tagged in 1995 and have been continually monitored ever since (Figure II-10). During the field season of 1996 a map of each individual's location within each plot was created. When individuals died or lost their tags, replacement individuals were chosen. Preference was given to replacement individuals of good health and in an easy to monitor location. When available three individuals of each species within a plot were monitored at all times.

II.3.1 Phenologic Monitoring

Plant development was followed throughout the entire summer. Plant phenophases were determined based on species morphology and ease of measurements (Table II-3) (Molau 1993b). Individuals were monitored daily at the beginning of the season and every second or third day during times of slow change.

II.3.2 Vigor Monitoring

Vigor measurements such as height, length of longest leaf, and number of leaves were measured only once at the end of each field season. All measurements were taken within approximately one week of August 18th on both years. For a complete listing of all vigor measurements collected see Table II-4 (Molau 1993b).

A

	Can sta			Erio tri			Erio rus			Dup fish			Sax hie			Sax hir		
P1																		
P2	181	181	183	181	182	182	187			177	179	183	177	178	179			
P3				•	•								184	185				
P4				194	199								187	188				
P5				209	206								198	197				
P6					223								198	198				
P7																		
P8																		
P9																		
		E18		0	E18	0	0	E18	0	0	E18	0	0	E18	0	0	E18	0
Q1				11	12	9.4				9	8.4	6.3	4.7	5	2.8			
Q2				2	2	3				2	2	3	6	5	7			
Q3				1	3	2							15	19				
Q4				7.5	7.7								11	17				
Q5				3	3													
Q6	10	12	16															

	Sax fol			Sax cer			Can pra			Jun big			Cal hom		
P1															
P2	181	182	182	182	182	182	178	179	181	187	190	199			
P3			183					196							
P4			187					198							
P5			206												
P6			235												
P7															
P8															
P9															
	0	E18	0	0	E18	0	0	E18	0	0	E18	0	0	E18	0
Q1	1.6	0.5	1.4	0.4	0.8	0.7	4.7	6.7	2.3						
Q2			9.3	2	2	2	1	7	3						
Q3															
Q4								3							
Q5															
Q6															

	Hie pau			Cen			Coc off			Dra.			Ste			Luzi arc		
P1																		
P2	185	187	187	181			181	181	181	•			178	182	182	181	181	181
P3									186	•								
P4									187	•								
P5									195	198								
P6									207	204								
P7																		
P8																		
P9																		
	0	E18	0	0	E18	0	0	E18	0	0	E18	0	0	E18	0	0	E18	0
Q1							2.3	2.4	1.7	1						2.7	2.2	3.2
Q2									7.8	6								
Q3									26	4								
Q4																		
Q5																		
Q6																		

	Pod X			Luzi con			Ran niv			Cansub					
P1															
P2															
P3															
P4															
P5															
P6															
P7															
P8															
P9															
	0	E18	0	0	E18	0	0	E18	0	0	E18	0			
Q1															
Q2															
Q3															
Q4															
Q5															
Q6															

B

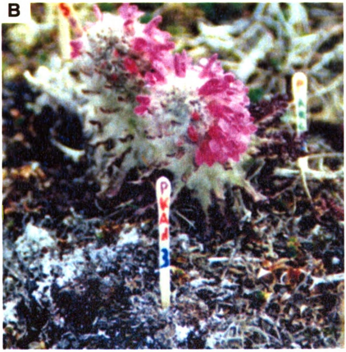


Figure II-10. Representation of the plant monitoring scheme: (A) recording sheet, (B) marked individual, and (C) map of plot.

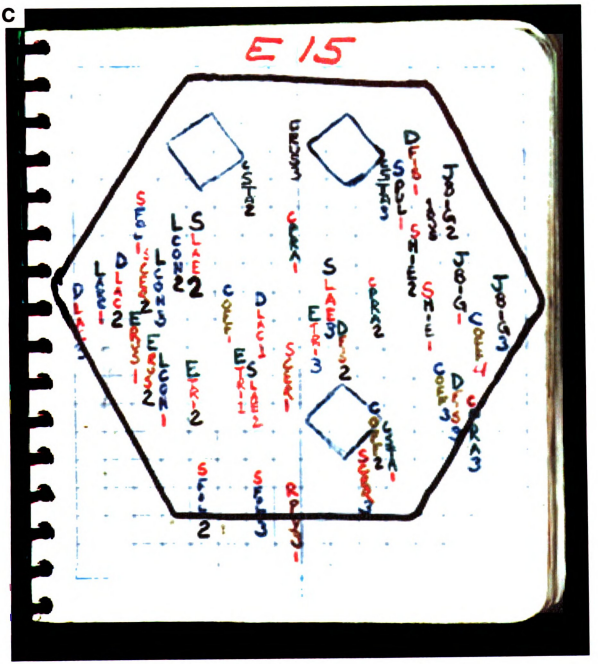


Figure II-10. Continued:

Table II-3. Phenologic measures recorded for all species monitored.

	Date snow free		Emergence of first green leaf		First bud/ inflorescence/ visible		First elongation of pedicules		First flower open		First stigmas visible		First anthers		First pollen shed		Withering anthers		First Flower Withering		Capsules emergence		First color change	
year	95	96	95	96	95	96	95	96	95	96	95	96	95	96	95	96	95	96	95	96	95	96	95	96
species																								
Alopecurus alpinus	X		X		X																			
Arctophila fulva	X		X		X		X																	
Calamagrostis holmii	X				XX		XX		XX		XX		XX				XX							X
Cardamine pratensis	X		XX		XX				XX										XX		XX			
Carex stans	X		XX		XX						XX		XX				XX							XX
Carex subspathacea	X		XX		XX						XX		XX				XX							XX
Cerasiutm beeringianum	X		XX		XX				XX										XX		XX			
Cochlearia officinalis	X		XX		XX		XX		XX						XX				XX		XX			
Draba lactea	X		XX		XX		XX		XX								XX				XX			
Draba micropetala	X		XX		XX		XX		XX								XX				XX			
Dupontia fisheri	X		XX		XX		XX				XX		XX				XX							XX
Eriophorum russeolum	X		XX		XX		XX				XX		XX				XX							
Eriophorum triste	X		XX		XX		XX				XX		XX				XX							
Eriophorum scheuchzeri	X		XX		XX		XX				XX		XX				XX							
Hierochloe pauciflora	X		X		X		XX				XX		XX				XX							
Juncus biglumis	X		XX		XX		XX						XX				X				XX			
Luzula arctica	X		XX		XX		XX				XX						XX		XX					
Luzula confusa	X		XX		XX		XX				XX						XX		XX					
Petasites frigidus	X		XX		XX		XX		XX		XX								XX					
Poa arctica	X		XX		XX		XX		XX		XX		XX				XX							
Ranunculus nivalis	X		XX		XX										XX				XX		XX		XX	
Ranunculus pygmeus	X		XX		XX										XX				XX		XX		XX	
Salix pulchra	X		XX		XX						XX										XX		XX	
Salix rotundifolia	X		XX		XX						XX										XX		XX	
Saxifraga caespitosa	X		X		X		X		XX		X				X				X					
Saxifraga cernua	X		XX		XX		XX		XX		XX				XX				XX				XX	
Saxifraga foliolosa	X		XX		XX		XX		XX		XX								XX				XX	
Saxifraga hieracifolia	X		XX		XX		XX		XX		XX								XX				XX	
Saxifraga hirculus	X		XX		XX				XX										XX		XX			
Stellaria humifusa	X								X										X					
Stellaria lactea	X		XX		XX		XX		XX		XX								XX					

Table II-4. Vigor measures recorded for all species monitored.

	Length of inflorescence		Length of longest leaf		Number of green leaves		Number of brown leaves		Number of flowers /individual		Number of inflorescences /plot		Number of buds /plot		Number of flowers /plot	
year	95	96	95	96	95	96	95	96	95	96	95	96	95	96	95	96
species																
Alopecurus alpinus	X		X													
Arctophila fulva	X		X													
Calamagrostis holmii	X		X								XX					
Cardamine pratensis	XX		XX		XX				XX		XX					
Carex stans	XX		XX		XX		XX		XX		XX					
Carex subspathacea	XX		XX								X					
Cerasiutm beeringianum													XX		XX	
Cochlearia officinalis	XX		XX						XX							
Draba lactea	XX		XX						XX							
Draba micropetala	XX		XX						XX							
Dupontia fisheri	XX		XX		XX						XX					
Eriophorum russeolum	XX								XX		XX					
Eriophorum triste	XX		XX		XX				XX		XX					
Eriophorum scheuchzeri	XX								XX		XX					
Hierochloe pauciflora	XX								XX		XX					
Juncus biglumis	XX										X					
Luzula arctica	XX		XX								X					
Luzula confusa	XX		XX								X					
Petasites frigidus	X		XX								XX					
Poa arctica	XX		XX								X					
Ranunculus nivalis	XX		XX		XX						XX					
Ranunculus pygmeus	XX		XX								XX					
Salix pulchra			XX								XX					
Salix rotundifolia			XX								XX					
Saxifraga caespitosa	XX		XX								XX					
Saxifraga cernua	XX		XX		XX						XX		XX		XX	
Saxifraga foliolosa	XX		XX								XX		XX		XX	
Saxifraga hieracifolia	XX		XX		XX				XX							
Saxifraga hirculus	XX												XX		XX	
Stellaria humifusa													XX		XX	
Stellaria lactea													XX		XX	

II.4 Data Analysis

The basic experimental design was a non-orthogonal completely randomized design with subsampling. The design was repeated in two field seasons. For statistical tests, plots were treated as the experimental units with multiple individuals within a plot treated as observational units used to obtain an estimate of observational error. Proper analyses of variance were run per species per variable. The homogeneity of the variances for all analyses was tested. In many cases this assumption was violated and the analyses were rerun with weighted averages adjusted by the population's standard deviation. In no cases were the conclusions different for the two analyses. Deviations from standard tests are noted. Population averages and errors of the sample means were used for all graphs; these calculations did not account for subsampling and weigh every individual observation equally. An outcome was deemed statistically significant if the probability for a Type I Error was 5% or less. Calculation of descriptive statistics including means, maxima, minima and standard deviations was done in Microsoft Excel 97 or SAS 6.12 (Microsoft 1997, SAS Institute 1990). All statistical tests were preformed in SAS by using proc GLM or proc MIXED (SAS Institute 1990, 1996). Proc GLM uses a general linear model and it was used to run analysis of variance with unbalanced data. Proc MIXED was used to run analysis of variance on correlated data using repeated measures.

II.4.1 Active Layer Comparisons

The active layer thickness data were analyzed in proc MIXED using the "repeated" statement (SAS Institute 1996). The active layer thickness at any given plot was correlated with measurements at the same point taken at other times during that field

season. Active layer thickness was not presumed correlated across years because of differences in climatic attributes known to affect soil freezing such as winter air temperatures and snow cover. The correlation pattern used was a continuous auto-regressive model as a function of Julian days. The SAS code used was:

```
proc mixed data = mydata.active;
  class year treat julian plot;
  model thaw = year treat plot year*treat
               julian(year) treat*julian(year);
  repeated / type=sp(exp)(time) subject=year*treat*plot ;
run;
```

II.4.2 Plant Comparisons

Analyses of the response variables were run identically for all species. Exemplary analyses were run to examine statistical significance when differences in variance were accounted for. These analyses were never significantly different from the original analyses and are therefore not presented.

The standard analysis run on each species was an analysis of variance run accounting for uneven replication numbers and subsampling sizes. The SAS code for this analysis was:

```
proc glm data = mydata.speciesdb;
    class year plot treat;
    model <RESPONSE VARIABLE> = year treat treat*year
                                plot(treat*year);
    test h = year treat treat*year e = plot(treat*year);
  by genspp;
    means treat*year;
    lsmeans treat*year /stderr e=plot(treat*year);
run;
```

The standard analyses run all species at once to determine overall significance was an analysis of variance run in proc MIXED. These analyses also accounted for unbalanced sample sizes and subsampling. The SAS code for the overall tests was:

```
proc mixed data = mydata.speciesdb;
    class year treat plot genspp;
    model <RESPONSE VARIABLE> = year treat genspp
                year*treat year*genspp treat*genspp
                year*treat*genspp;
    random   plot(genspp) plot(year) plot(treat)
             plot(year*treat) plot(year*genspp)
             plot(treat*genspp);
run;
```

The analysis run to compare the 1995 open-top chamber (OTC) with the 1996 control was used analysis of variance with unbalanced sample sizes. The "year" and "treatment" groups were combined to make four separate groups and each of these populations was tested to determine if the sample means were equal. Multiple comparisons were performed with Fisher's LSD (least significant difference) and Tukey's HSD (honestly significant difference) (SAS Institute 1990). In all cases the significances were similar for the two analyses. The SAS code used to compare the 1995 OTC with the 1996 control was:

```
proc glm data = mydata.speciesdb;
    class txyear plot;
    model <RESPONSE VARIABLE> = txyear plot(txyear);
    means txyear / e=plot(txyear) LSD lines;
    means txyear / e=plot(txyear) tukey lines;
  by genspp;
run;
```

(Note the variables treatment and year were combined in order to easily run this analysis)

The percentage of individuals flowering (presented in section IV.2.1) was calculated as the ratio of the number of individuals for which the flower opened to the number of individuals monitored. Individuals that were found late in the season because

of the presence of an inflorescence were not included in this percentage. An analysis of variance was also run on this data set.

The percentage of individuals responding similarly (reported in section IV.4.3) were calculated by adding up the category presented from Tables IV-2 and IV-3 and dividing by the total.

Chapter III

ABIOTIC DOCUMENTATION AND CHAMBER PERFORMANCE

In this chapter the results of a detailed documentation of the abiotic environment surrounding the vegetation is presented. In addition the performance of the chambers is described in order to access the efficacy of the open-top chamber as a warming device.

III.1 CLIMATIC DATA

The 1996 field season was warmer than that of 1995. The temperature 13cm above the control plots was, on average, 1.2°C warmer (Table III-1). The field season of 1996 received almost twice as much precipitation as that of 1995 (Table III-1). It should be noted that the increased precipitation in 1995 might not have resulted in an increase in soil moisture because there may have been differences in runoff and evapotranspiration between the two years. The daily average maximum and minimum temperatures are given in Appendix Table A-1; the temperature from the nearby NOAA meteorological screen at 2 m above ground are also presented for comparison. It was found that plant canopy temperatures of the control plots during summer are generally 0.5-1.0 °C warmer than screen temperature.

On average, over the entire monitoring period, the chambers warmed the plant canopy 1.9°C in 1995 and 1.4°C in 1996 in the monitored chambers. The relative humidity was 7.3 % less than that of the controls in year 1996; this is commensurate with

an expected drop in relative humidity with increase in temperature. A more detailed description of the chamber performance is given in the next section.

Table III-1. Summer average, maximum, and minimum daily temperature and relative humidity of chambers and controls and climatological data of the nearby NOAA station from snowmelt until August 18th for 1995 and 1996.

	NOAA							Control						OTC					
	Precip (cm)	Temperature (°C)			Relative Humidity			Temperature (°C)			Relative Humidity			Temperature (°C)			Relative Humidity		
year		mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min
1995	18	3.2	6.0	1.4	89.4	98.8	—	3.6	7.7	0.4	—	—	—	5.5	12.2	0.8	—	—	—
1996	33	3.7	7.7	1.0	89.1	98.2	—	4.8	9.4	0.7	89.1	95.6	80.5	6.2	13.2	0.7	76.4	89.2	63.1

— data not available

III.2 CHAMBER PERFORMANCE

III.2.1 Temperature and Humidity

The OTCs passively warm the plant canopy by acting as miniature greenhouses. By their design, the OTCs are dependent on solar radiation for warming. On days of dominant cloud cover the chambers only marginally warm the plant canopy, while on sunny days the chambers substantially warm the canopy. During the summer "night," when the sun is at a low angle on the horizon, the chambers generally do not warm the canopy, thus accentuating the normal diurnal pattern of warming that occurs in the absence of a true night. This causes an increase in maximum daily temperatures but not the daily minimums. As expected, the relative humidity follows changes in temperature inversely. These patterns of warming and humidity are shown in Figure III-1 for three representative days. The daily course of warming in the chambers mirrors that of the controls and is strongly tied to incoming solar radiation. On all days the average

temperature within the chambers was greater than that of the controls. The spikes in the temperature trace changes in cloud conditions. The chamber response is sensitive to changes in radiation and shows a larger daily range of temperature than the control. There is also a greater daily variation of temperature in the chambers than the controls because the chambers warm substantially more on days with clear sky conditions.

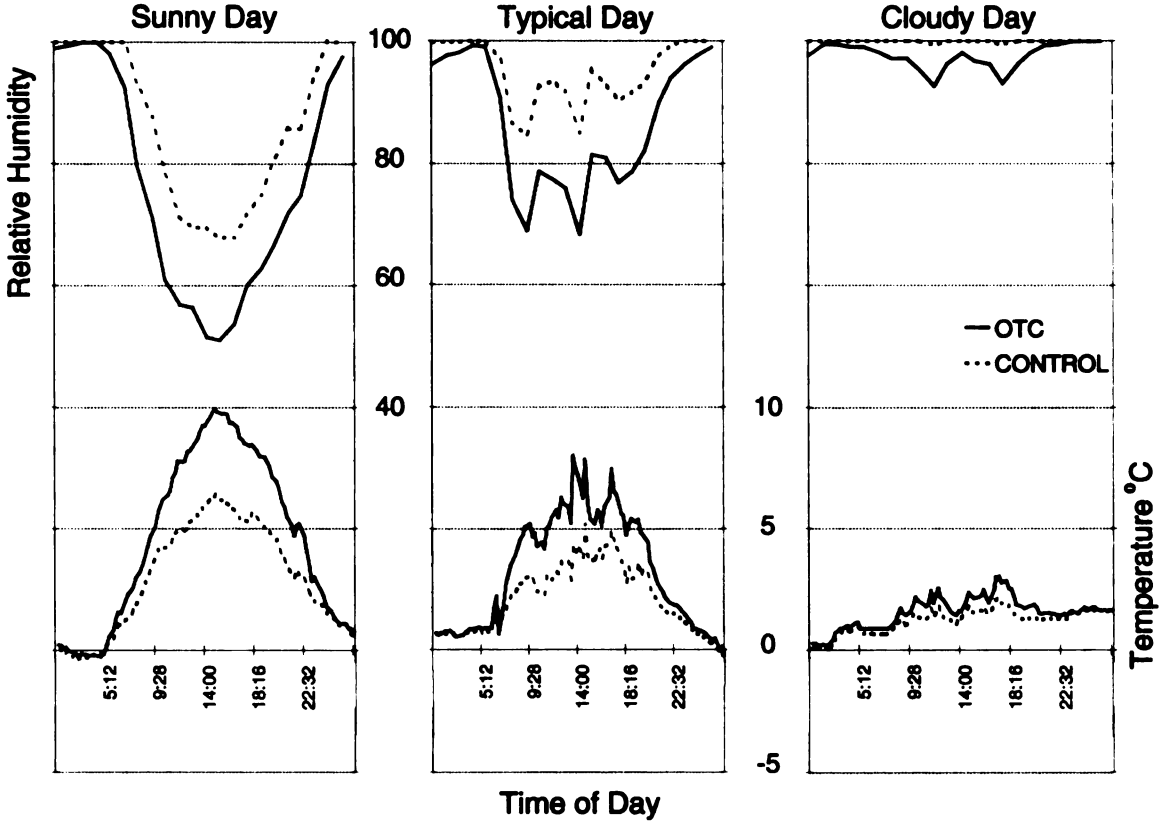


Figure III-1. The course of mean temperature and relative humidity in OTCs and control plots for three different types of days: a sunny day (8/8/95); a typical day (8/6/1995); and a cloudy day (7/30/95) (N for OTC =18; N for control = 18).

There are among-chamber differences in warming, presumably due to micro-topography and vegetation structure. This variation is similar to among-control plot variation but greater in magnitude. These differences are demonstrated in Figure III-2 by

examining the average, maximum and minimum temperature on a typical sunny day both over control plots and within OTCs; the range in the graph represents the two extreme monitored plots for each treatment.

III.2.2 Vertical and Horizontal Patterns of Chamber Warming

Vertical and horizontal patterns of warming were documented within the chambers (Figures III-3). These temperature distributions are presumably due to influences of shading, convection, and ventilation within the chambers. The north side of the chamber is warmer because direct radiation enters through the open top when solar radiation is greatest, around solar noon when the sun is in the south at a 42.5 degree angle or less (Figure III-4). The vertical temperature distribution within the chambers is notably different than the controls. Temperatures are warmer within the OTCs at all heights and the peak in warmth is at 16 cm height whereas under natural conditions it is warmest at the ground surface and becomes progressively cooler further from the surface (Figure III-3).

III.2.3 Light Distribution within a Chamber

Measurements of light showed that approximately 80% of the ambient solar radiation enters the chamber, and that these levels are not evenly distributed (Figure III-4). Due to the higher light intensity when the sun is to the south, the light levels are greater in the northern portion (83% of ambient) of the chamber and less in the southern portion (68% of ambient). Light levels are 93% of ambient in the center. These light levels are considerably different than the reported transmittance of the chamber material

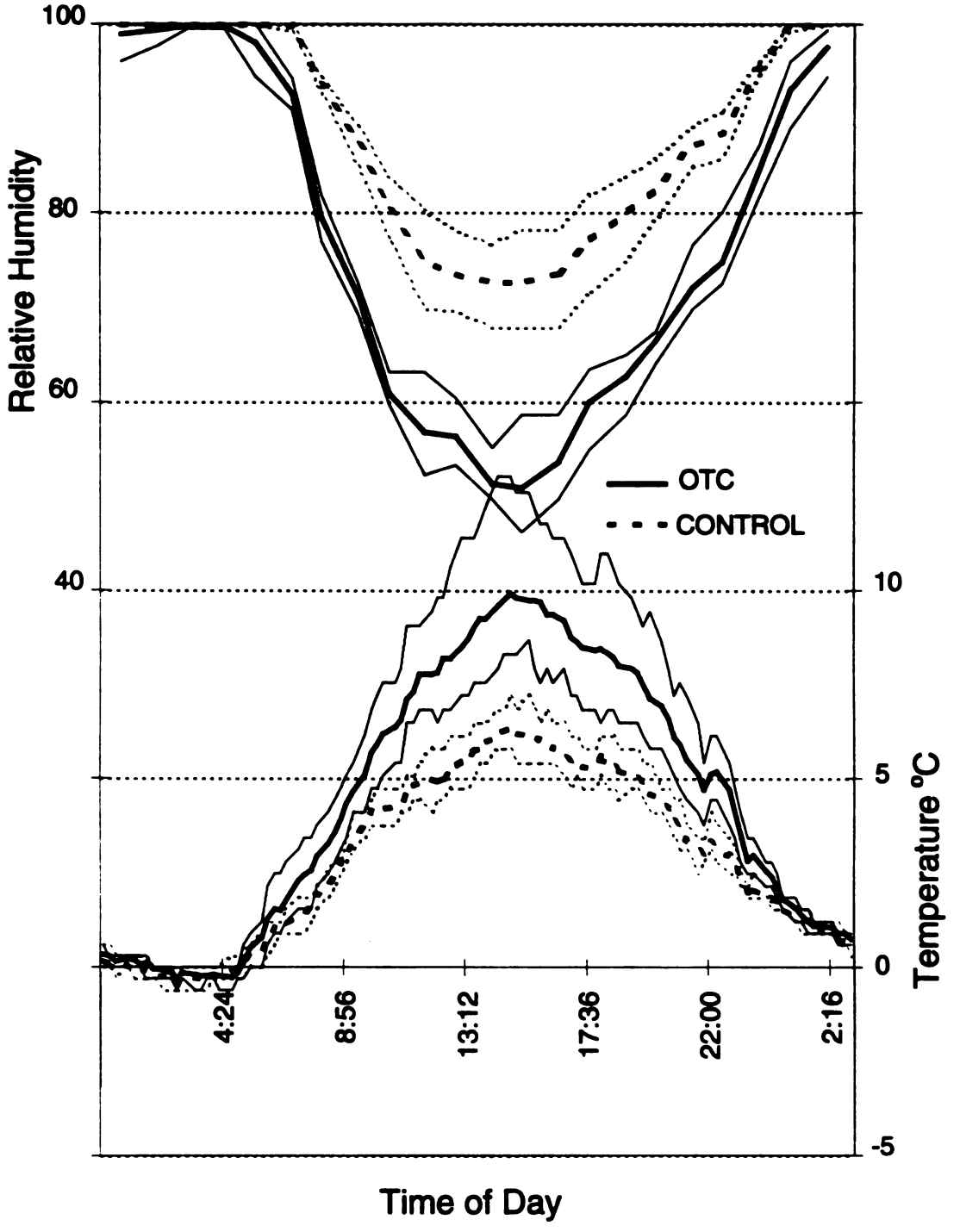


Figure III-2. The mean (thick line) and range (thin line) course of temperature and relative humidity in OTCs and control plots on a sunny day (8/8/95) (N for OTC = 18; N for control = 18).

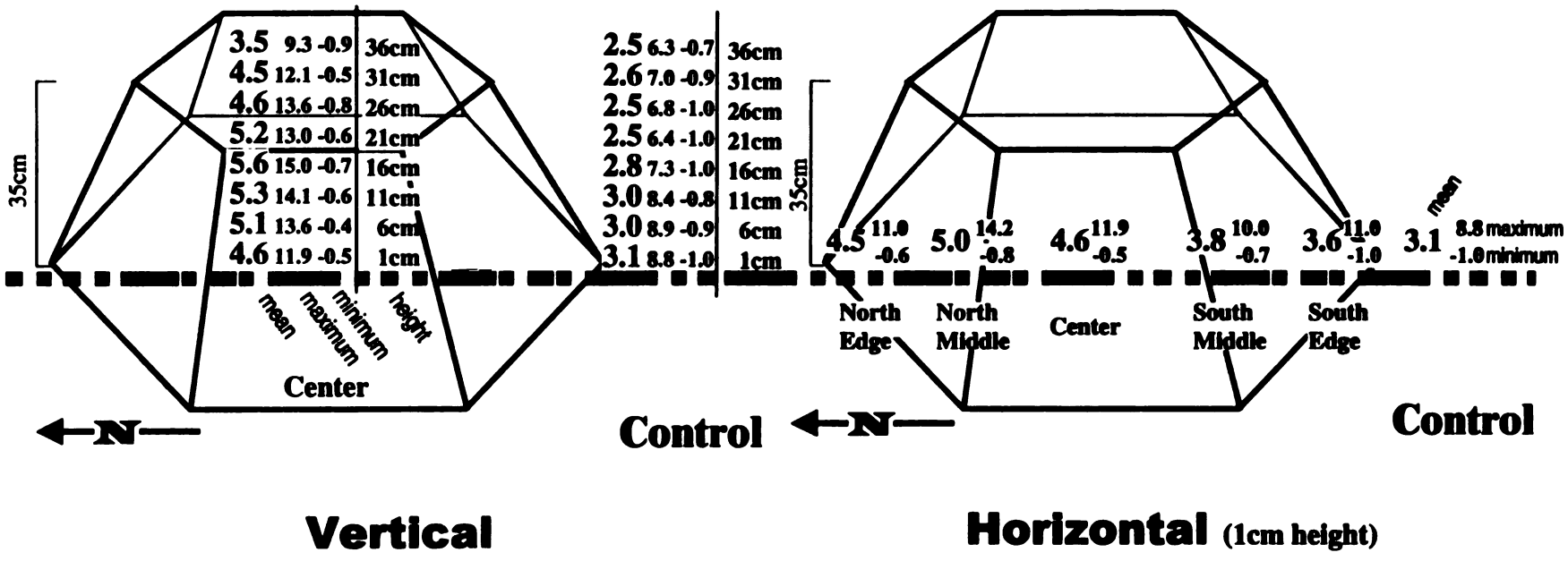


Figure III-3. The vertical and horizontal temperature distribution of the average daily mean, maximum and minimum within a chamber from June 20 - July 28, 1995 (N = 1).

of 86% in the visible wavelengths for several reasons: the StowAway™ light loggers used in the field measure a different range of wavelengths that are skewed towards the infrared (Appendix Figure A-5), the angle of the sides of the chambers to the sun does not allow for optimum transmittances, the chambers can be dirty or scratched, and most importantly the open top of the chambers allows direct light. Overall the chamber creates minimal shading, due to the of the high transmittance of the chamber material and the open top allows direct sunlight to nearly all portions of the chamber at some time during the daily solar cycle.

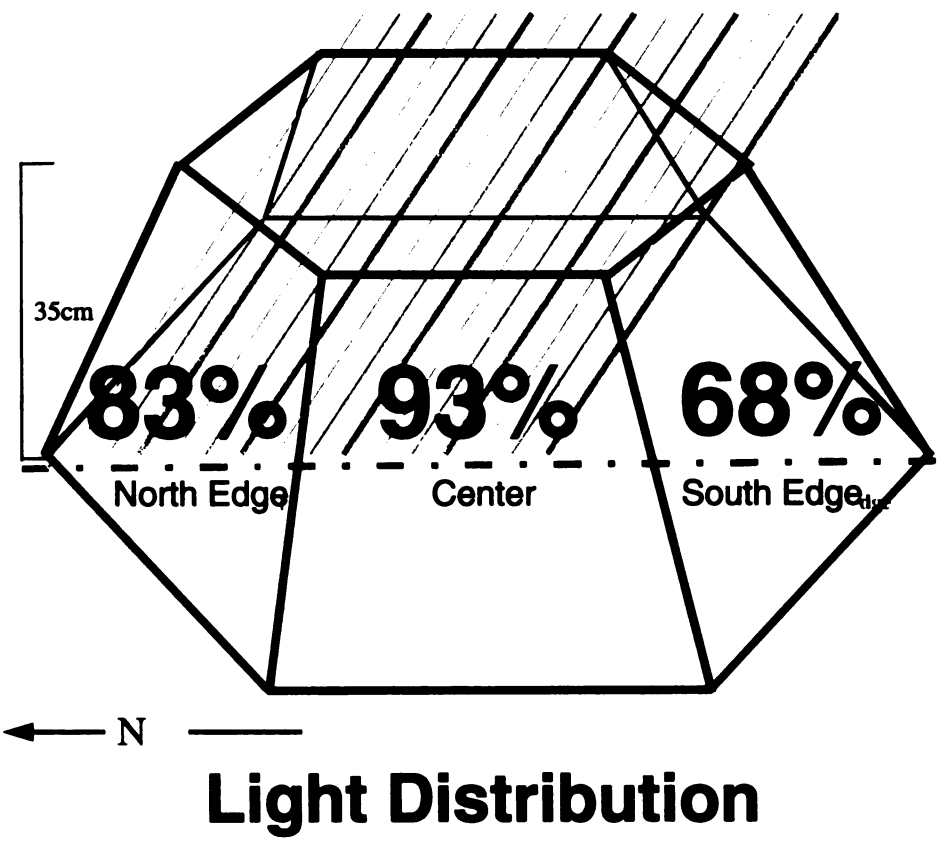


Figure III-4. Light distribution relative to natural conditions within a chamber from August 1 -21, 1996 (N =1 and N = 2 for the center).

III.3 Below Ground Responses to Temperature

III.3.1 Soil Temperature

The soil temperature was only sampled during one field season; thus the only comparison that can be made is between treatments. The chambers caused distinct soil warming in the wet meadow site in Barrow, Alaska. Warming was more pronounced in the upper layers of soils and gradually diminished with depth (Figure III-5). The increase in temperature was 1.2, 0.7, 0.4, 0.4, and 0.1°C for depths 1, 5, 10, 15, and 30cm respectively. There was considerably less soil warming under chambers in the ITEX dry heath community than in the wet meadow community (Walker 1997, Figure III-5).

III.3.2 Active Layer Thickness

The active layer development was significantly different between the two years. The warmer 1996 field season had a thicker active layer (Figure III-6, Appendix Table A-2). The active layer thickness did not show a statistically significant response to chamber warming. Plots were found to be significantly different from each other due to overall heterogeneity of site thaw patterns. Personal observations of differences up to 10cm in depth of thaw between points only a meter apart were not uncommon; Mueller (1996) also refers to such heterogenity in Barrow tundra. This may mask a small chamber effect that appears to be present at some times during the summer from an examination of Figure III-6.

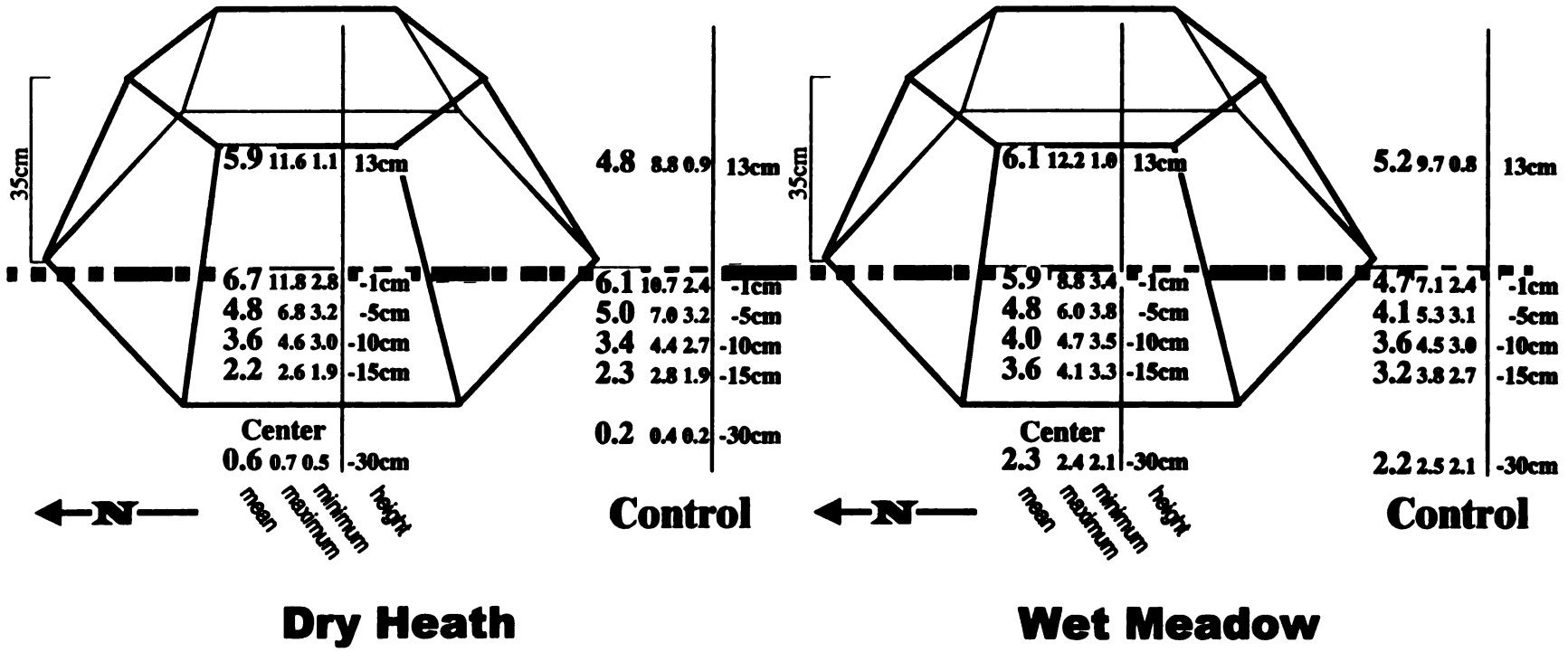


Figure III-5. Soil warming under the chambers in two community types and their respective controls. Data collected were from the same time period (July 10 – August 18, 1996) and the two chambers were within 100 meters of each other (N = 1).

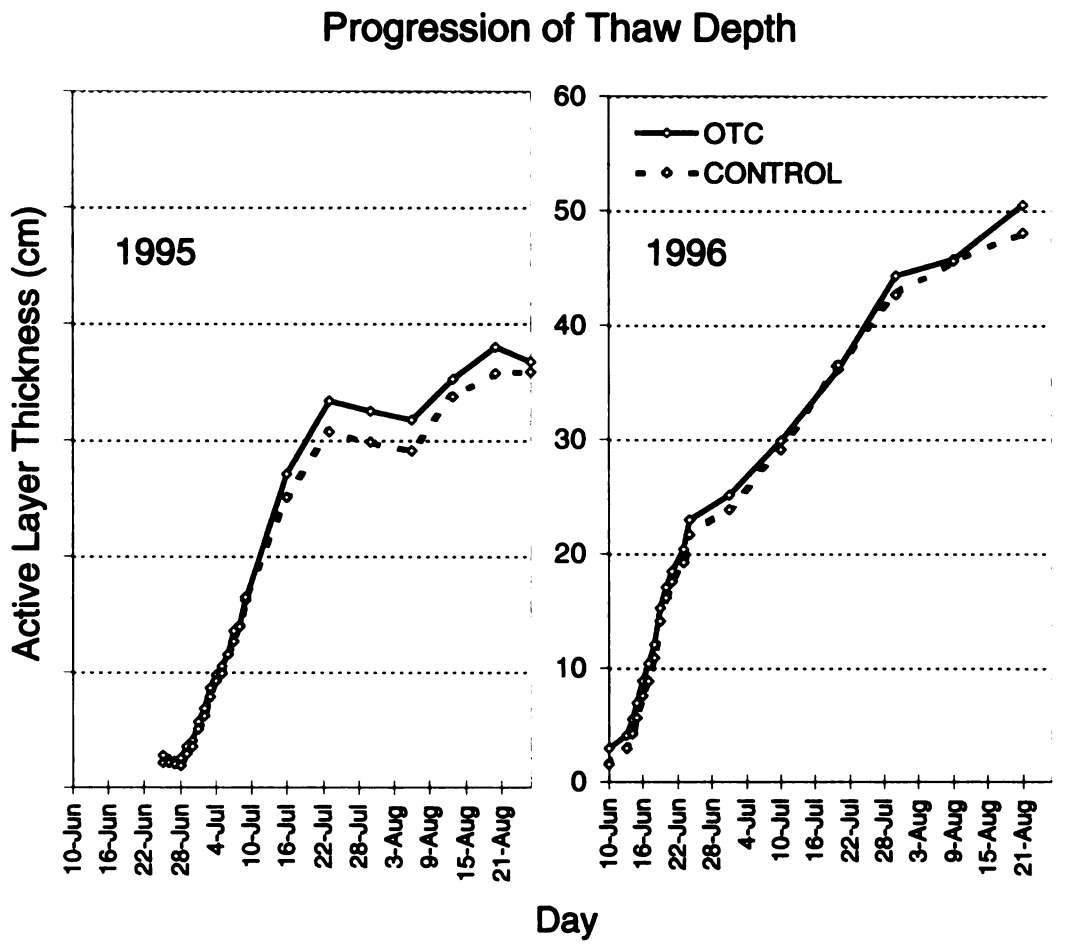


Figure III-6. Progression of active layer thickness throughout the 1995 and 1996 field seasons (N for OTC = 24; N for control = 96).

III.4 Accumulation of Thawing Degree Days

There were differences in the thawing degree day accumulation from snow melt (TDD*) between the two years. The 1996 field season was warmer than that of 1995 and had a longer growing season up until late August. Thawing degree days calculated from daily average temperatures from standard screen height measurements provided by NOAA show the accumulations through August 18 to be 212 and 282 for 1995 and 1996

respectively. These two field seasons show a higher trend in thawing degree day accumulation than the thirty year whole year average of 251 from 1941-1970 (Brown *et al.* 1980).

The documented increase in canopy temperature within the chambers although relatively small in absolute magnitude over the summer caused approximately a 38% and 30% increase in TDD* in years 1995 and 1996 respectively (Figure III-7). The among-plot differences in temperature reported in section III.2.1 are amplified when examining thawing degree days of the plots for the entire summer as seen in Figure III-7 examining the absolute range in TDD* per treatment. In addition the TDD* for the 1996 controls is similar in average and range to the 1995 open-top chambers; this will be useful for comparing the response of plant species comparisons in Chapter IV. The thawing degree day accumulations from June 19 – July 6, 1995 were estimated from screen height data provided by NOAA because data loggers had not been installed by this time, thus there are no differences between treatments in Figure III-7.

III.5 Discussion and Conclusions

The two field seasons showed considerably different weather conditions, which is in keeping with the known extreme variability in daily and interannual weather patterns for the Arctic. The average control plot temperature in 1996 of 4.8 °C was 1.3 °C warmer than that of 1995. The snow melt of the field site in 1996 was approximately 10 days earlier than in 1995. The combination of these factors caused an increase of 116 thawing degree days from snow melt (TDD*) up to August 18 in 1996 over 1995.

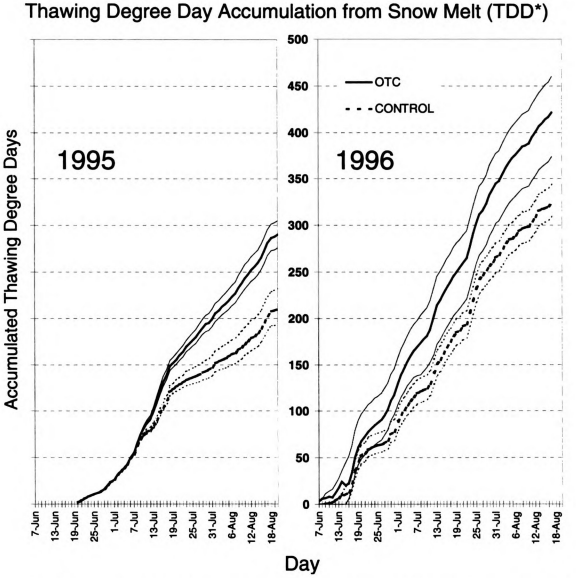


Figure III-7. Mean (thick line) and range (thin line) degree day accumulation from day of snow melt for the field seasons 1995 and 1996 ($N \geq 7$).

Total seasonal thawing degree day accumulation is not a useful predictor of plant response because dormancy or senescence generally begins in mid August, thus accumulations after this stage have little effect on the plant. For example, from personal observation, well formed buds of *Cardamine pratensis* in late August of 1995 did not flower that September; rather, they over-wintered and flowered feebly in June of 1996 without setting seed. For these reasons and those given on page 38 all end-of-season vigor measures were compared with TDD* up until August 18 not total season thawing degree days. Due to seredipidity, the 1996 controls had a similar degree day accumulation to the 1995 OTCs. This created an opportunity to test the efficacy of the chambers as a temperature enhancement device. If the plants responded similarly to degree day accumulation for both treatments, then it is reasonable to conclude that the plants were responding to temperature and not to some other chamber effect.

The increased warming and near-ambient solar radiation levels in the northern center of the chamber has the potential to cause greater plant response in this region of the chamber. The temperature peak at a height of 16cm as opposed to ground surface under the control should not noticeably disrupt the natural heat differential in plant tissues because plant tissue temperature is highly dependent on solar radiation that naturally has high variability (Hanson 1973). The measurements of vertical and horizontal distribution of warming was conducted in a nearby location with less plant canopy and some exposed bare ground; we would expect a different temperature distribution within the wet meadow site because of the dominant plant canopy (Bay 1996). Therefore, the results are only demonstrative of the general chamber performance and do not represent exact details of response in the wet meadow itself.

The chambers produce more variability in temperature than seen in the control plots in both time and space. The chambers have higher daily maxima, which are highly dependent on sky conditions, leading to large among-day variation. The horizontal distribution of temperature within a chamber and the among-chamber differences are greater than the among-control differences. Due to the greater variability of temperature in the chambers, we would expect a greater variability of plant response within the chambers if temperature is a major controller of plant response. Furthermore, the increase in range of variability within chambers is commensurate with climate warming predictions that also call for an increase in the variability of weather events (Karl *et al.* 1995).

The lower light levels reported in the chambers are not considered to be of great concern to plant performance. The vast majority of experiments involving the manipulations of light levels in the Arctic show no detectable effects of minimal shading (Savile 1972, Chapin *et al.* 1995). Temperature and nutrient levels are believed to be more limiting factors than light in this system, although light levels could become an important factor when temperature and nutrient limitations are minimized. Yet this is unlikely with the small levels of shading occurring within the chambers and the natural heterogeneity in light levels due to natural canopy shading.

There were differences between the wet meadow and dry heath communities in terms of soil warming under the chambers. The ground's surface is warmer in the dry heath community and there are considerable differences in soil temperatures with depth under ambient conditions. The soil temperature profiles of the two sites suggest that the soils of wet meadow conduct heat more than the soils of the dry heath and supports the

well-established notion that the heat diffusivity of soils is highly dependent on soil moisture (Nelson *et al.* 1985). The dry heath site showed very little if any soil warming (Walker 1997). No soil warming under a similar chamber was documented by Wookey *et al.* (1993) in a dry heath site in Abisko. Wookey *et al.* (1993) attributed no soil warming to be primarily due to reduced convective heat transfer because the chambers greatly reduce wind. The dry heath community has a significant amount of bare ground. This exposed ground is highly receptive to wind and direct solar radiation, both of which are reduced by the chambers. In the wet meadow convective and radiative heat transfer are proportionally less important due to the dense plant canopy, thus the soils in the wet meadow are warmer than ambient under the chambers and the soils in the dry heath are not.

The small size of the chambers presumably does not allow for increased progression of active layer thickness, despite documented soil warming in the upper soil layers in the wet meadow site. The chamber warming apparent in surface temperatures under the chamber in the wet meadow diminishes with depth. Hysteresis from the mass of permafrost around the chambers may dampen the small potential changes in active layer thickness due to warming. Changes are also difficult to detect as a result of the heterogeneity of the permafrost (Mueller 1996). There are clear annual differences in active layer thickness as shown in the comparison of 1995 and 1996. These difference may be attributed to many factors including length of growing season, soil moisture, snow cover, and winter temperature in addition to summer air temperatures (Smith 1975, Shiklomanov 1997).

The changes in soil temperature and the potential for changes in active layer thickness are of importance because of their potential to change nutrient availability and turnover rates in the system (Hobbie 1996). Tundra systems are widely believed to be nutrient limited, and changes in nutrient availability have been shown to cause significant changes in vegetation (Chapin 1987, Jonasson 1992). The potential for the uncoupling of below ground warming and canopy is the most notable limitation of the chambers. Understanding the dynamics of the below ground system and its links to warming are critical if chambers are to be used to predict species response to global warming. Fortuitously, there are measurable increases in soil temperature in the wet meadow site at shallow depths, were most biological activity occurs, and this warming is in accordance with predictions of increased soil temperatures associated with climate warming. Although this warming effect diminishes with depth and does not create a corresponding increase in active layer thickness, it causes less concern here than it does for sites that do not show warming, such as the dry heath site in Barrow.

There are other documented limitations of the OTCs. Marion *et al.* (1993) recorded night time cooling and Jones *et al.* (1997) found evidence for reduced pollination; however, neither of these phenomena have been observed at Barrow. This thesis has attempted to address the key concerns presented by critics such as Kennedy (1995) about the use of chambers: the chambers were installed during the snow free period only to avoid unnatural snow accumulations and winter microclimates; temperature and humidity was monitored throughout the entire season; and light, soil temperature, and temperature distribution within a chamber was monitored. The most notable limitation of the chambers is the lack of a true control for temperature because

they manipulate more than temperature. These secondary effects, including shading and reduced wind, make conclusions based on plant response to chambers not solely attributable to temperature.

These studies suggest that the use of the OTCs is valid and that they are an appropriate tool to produce summer warming. Further, the warming levels of 1.5 - 1.9 °C are in the range predicted by global climate simulations (Chapman and Walsh 1993, Houghton *et al.* 1996). It is believed that discoveries based on short-term plant response to chambers coupled with natural interannual variation will be of use in understanding plant temperature relations and that long-term plant response to chambers coupled with latitudinal comparisons will be of use in forecasting vegetation response to climate warming.

Chapter IV

PLANT RESPONSES TO TEMPERATURE

In this study, all species contained within the site were monitored for many phenologic and vigor measures (Tables II-5 & II-6). The analysis presented will be restricted to those species with sufficient replicates to confidently form conclusions. This reduces the database from thirty one to thirteen species. For several of the species, the flowering variables are not discussed because of limited sample sizes resulting from the episodic nature of arctic flowering or their low frequency in the plots. Analyses were run separately on each species, and then rerun for overall significance for all species in a combined data set (see section II.4.2).

IV.1 RESPONSE OF FLOWERING PHENOLOGY

Question: In what way and to what extent will the phenology of selected plants respond to variations of growing season temperature and increased canopy temperature?

IV.1.1 Hypothesis 1a: *Flowering will occur earlier under warmer conditions.*

The onset of flowering for all species monitored is presented in Figure IV-1. All of the species flowered significantly earlier during the warmer year of 1996 than the cooler year of 1995 and half flowered significantly earlier in the chambers during those years. The combined overall analysis found year but not treatment differences to be significant. In all but two species, *J. biglumis* and *E. triste,* the average date of flower opening was earlier in chambers than the control of that season; furthermore, this

difference was significant in *C. pratensis*, *S. hirculus*, *L. arctica*, *L. confusa*, *H. pauciflora*, and *D. fisheri*. The two species that did flower on average marginally earlier in the controls, *E. triste* and *J. biglumis*, flowered earlier in the OTC's the following year. *J. biglumis* was the only species to show a significant interaction between year and treatment.

IV.1.2 Hypothesis 1b: *Flowering will occur at approximately the same degree day threshold.*

Flowering was analyzed in terms of thawing degree days since snow melt (TDD*) in order to examine temperature relations. If accumulated temperature is significant in controlling plant development than flowering should occur at the same degree day accumulation for all treatments and years rather than calendar (Julian) date. When examining the date of flower opening in terms of TDD* rather than Julian days interannual variability was found to be much less significant across species (Figure IV-2). Year was found to not be significant overall; although *S. hieracifolia*, *S. hirculus*, *J. biglumis*, *H. pauciflora*, and *D. fisheri* showed year as a significant effect on the TDD* date of flowering. Treatment generally affected flowering and was found to be overall significant. For all species within a given year it took on average more degree days for a flowering to occur within chambers. For half of the species this effect was significant. Although there are often significant chamber and year effects, the magnitude of these effects is much less in terms of TDD* than Julian days.

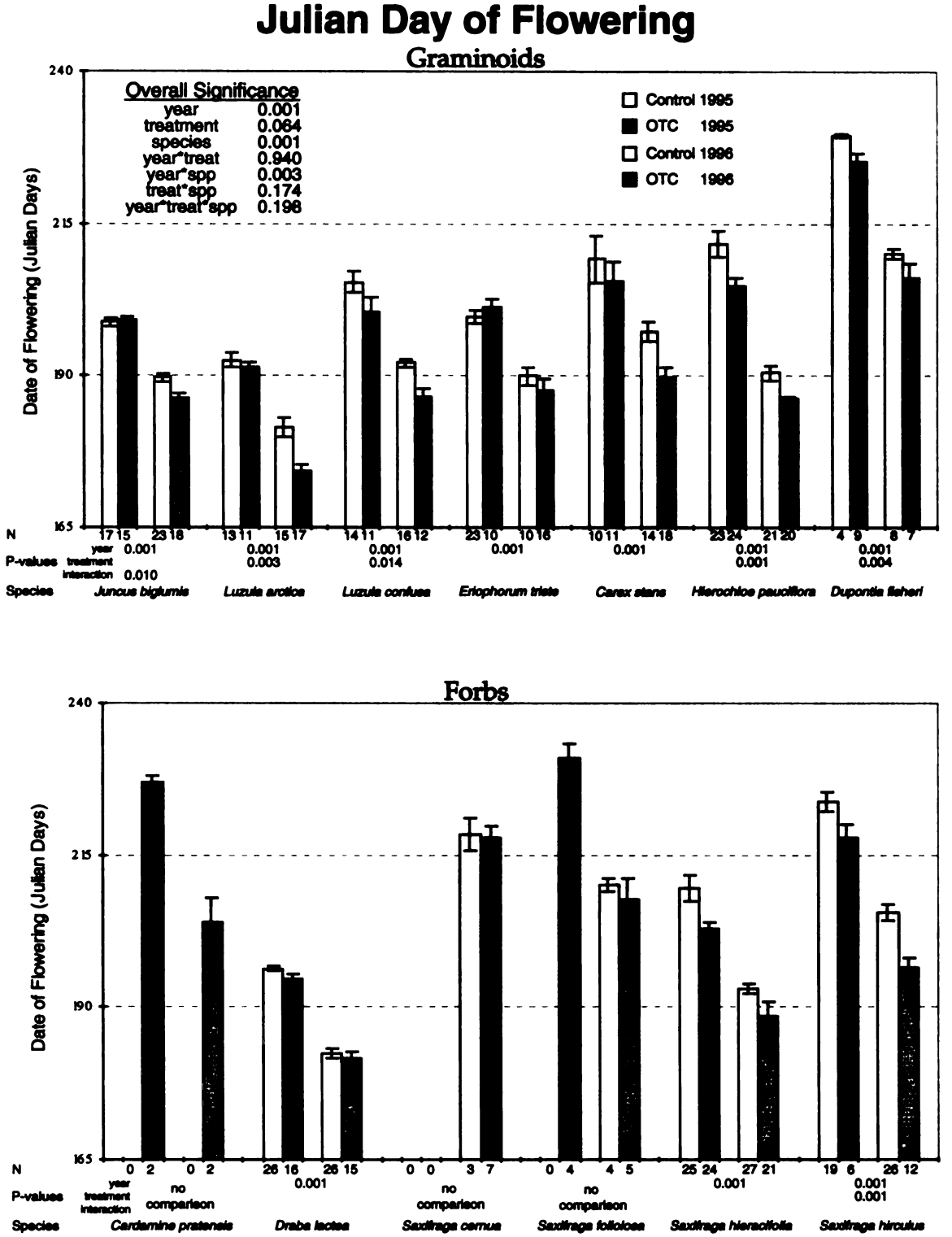


Figure IV-1: Julian date of flowering for all species. Histogram bars represent averages, with standard error of the mean as error bars. P-values of less than 0.05 reported from a two way ANOVA and samples size are given for each species. Overall significance (top left) is reported from a three way ANOVA run on all forbs and graminoids.

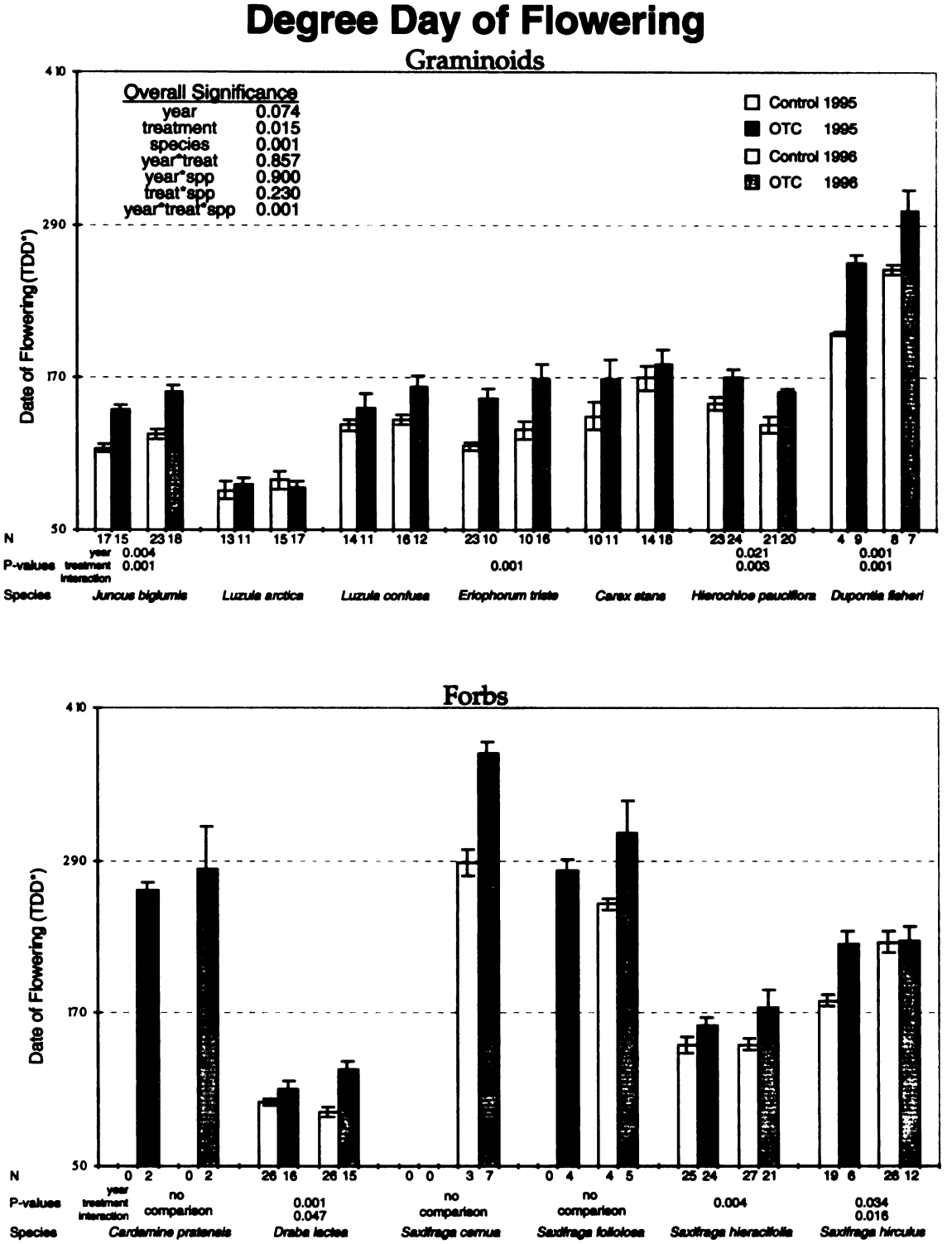


Figure IV-2: Degree day of flowering for all species. Histogram bars represent averages, with standard error of the mean as error bars. P-values of less than 0.05 reported from a two way ANOVA and samples size are given for each species. Overall significance (top left) is reported from a three way ANOVA run on all forbs and graminoids.

IV.2 VIGOR RESPONSE

Question: In what way and to what extent will the vigor of selected plants respond to variations of growing season temperature and increased canopy temperature?

IV.2.1 Hypothesis 2a: *Plant will produce more flowers under warmer conditions.*

Of the six species for which the number of flowers was measured there was no consistent pattern in flower numbers within the plots in response to temperature (Figure IV-3). The three species, *S. foliolosa, S. cernua* and *D. fisheri,* flowered more in the warmer year and *C. stans* and *H. pauciflora* significantly flowered more in the chambers. *C. pratensis* and *S. hirculus* did not respond to either of the treatments or year. Overall year was found to be significant but treatment was not. Furthermore, the average number of flowers was found to be greater within the control than within chambers for *D. fisheri* and *S. hirculus* in 1996. There was considerable variation of flowering between plots and this measure was not recorded for all species; therefore statistical comparisons were of low power.

An examination of the percentage of monitored individuals that flowered also shows no clear pattern in response to interannual variability or canopy warming (Table IV-1). Some species flowered at a higher percentage during the cooler year of 1995 and some flowered more in 1996; some species flowered more in the controls and others flowered more in the chambers. Neither year nor treatment were significantly different in the percentage of individuals flowering, based upon the results of an ANOVA.

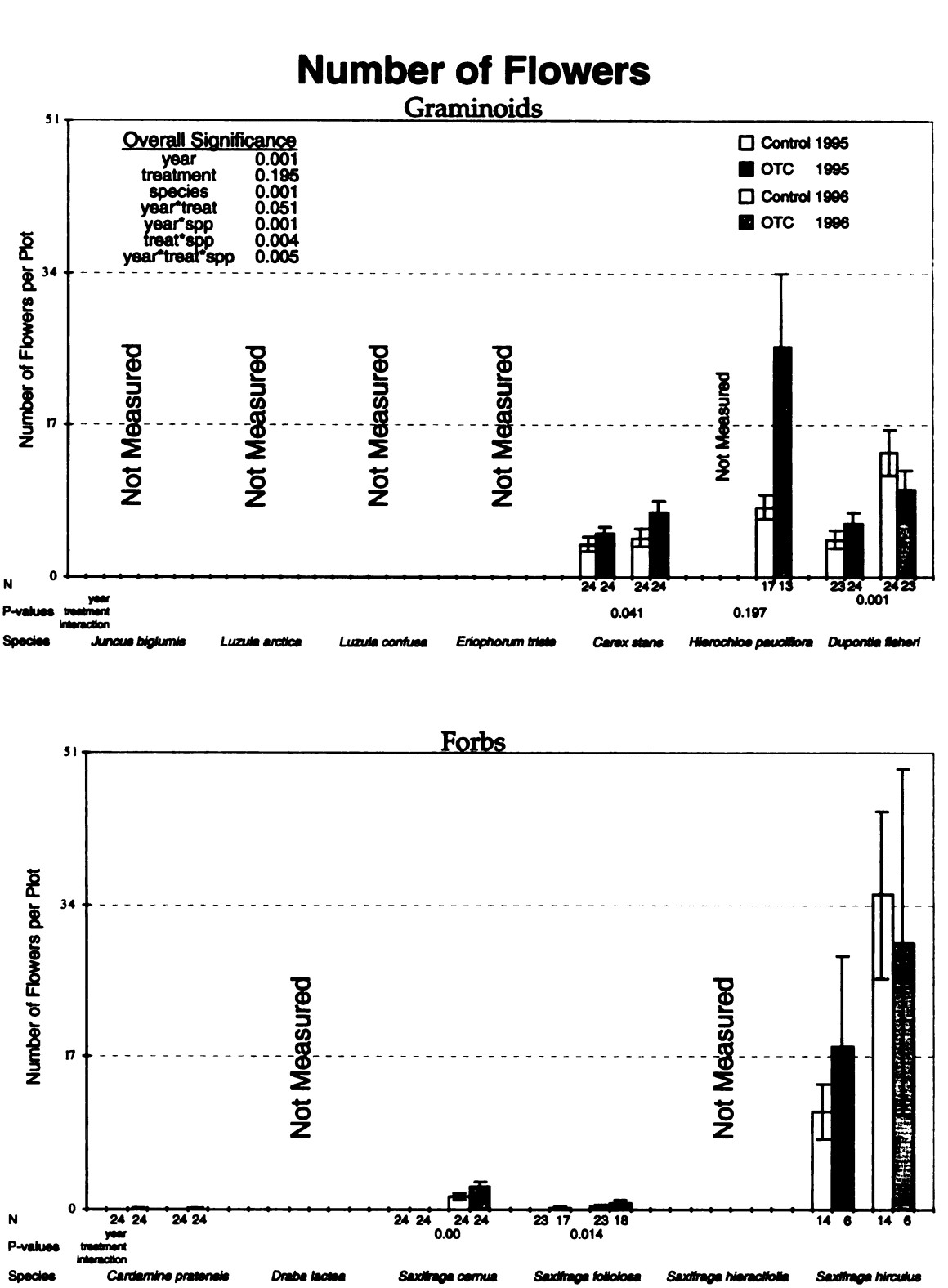


Figure IV-3. Number of individuals flowering within a plot. Histogram bars represent averages, with standard error of the mean as error bars. P-values of less than 0.05 reported from a two way ANOVA and samples size are given for each species. Overall significance (top left) is reported from a three way ANOVA run on all forbs and graminoids.

Table IV-1. Percentage of monitored individuals that flowered during the two years in both treatments.

	1995		1996		
Species	Control	OTC	Control	OTC	Average
Cardamine pratensis	0.0	2.8	0.0	2.9	1.5
Carex stans	13.6	15.3	20.0	25.0	18.6
Draba lactea	81.8	80.0	82.1	87.5	82.7
Dupontia fisheri	5.6	12.9	12.9	10.9	10.4
Eriophorum triste			Not Measured		
Hierochloe pauciflora			Not Measured		
Juncus biglumis	81.3	42.9	61.8	50.0	58.5
Luzula arctica	46.4	43.5	38.7	69.6	48.6
Luzula confusa	50.0	37.5	50.0	52.9	48.9
Saxifra cernua	0.0	0.0	4.5	10.1	3.6
Saxifraga foliolosa	0.0	8.9	6.1	10.4	5.8
Saxifraga hieraciifolia	72.7	82.8	77.1	67.7	75.0
Saxifraga hirculus	55.9	40.0	72.2	80.0	63.0
Average	37.0	33.3	38.7	42.5	37.9

IV.2.2 Hypothesis 2b: *The height of inflorescence will be taller under warmer conditions.*

The length of inflorescence was consistently longer during the warmer field season and within chambers (Figure IV-4). Both year and treatment were found to be significant overall. All species for which there were adequate replicates but two, *E. triste* and *S. hirculus*, significantly responded to both treatment and year. For all species the average height was greater in the chambers and during the warmer field season of 1996. This is demonstrated by the step-like pattern in Figure IV-4 the different treatments in different years going from control 1995 to OTC 1996. This pattern is very similar in direction and relative magnitude to the pattern of degree day accumulation for the years and treatments (see section III.3). Furthermore, many of the species responded similarly in the OTC of 1995 and controls of 1996.

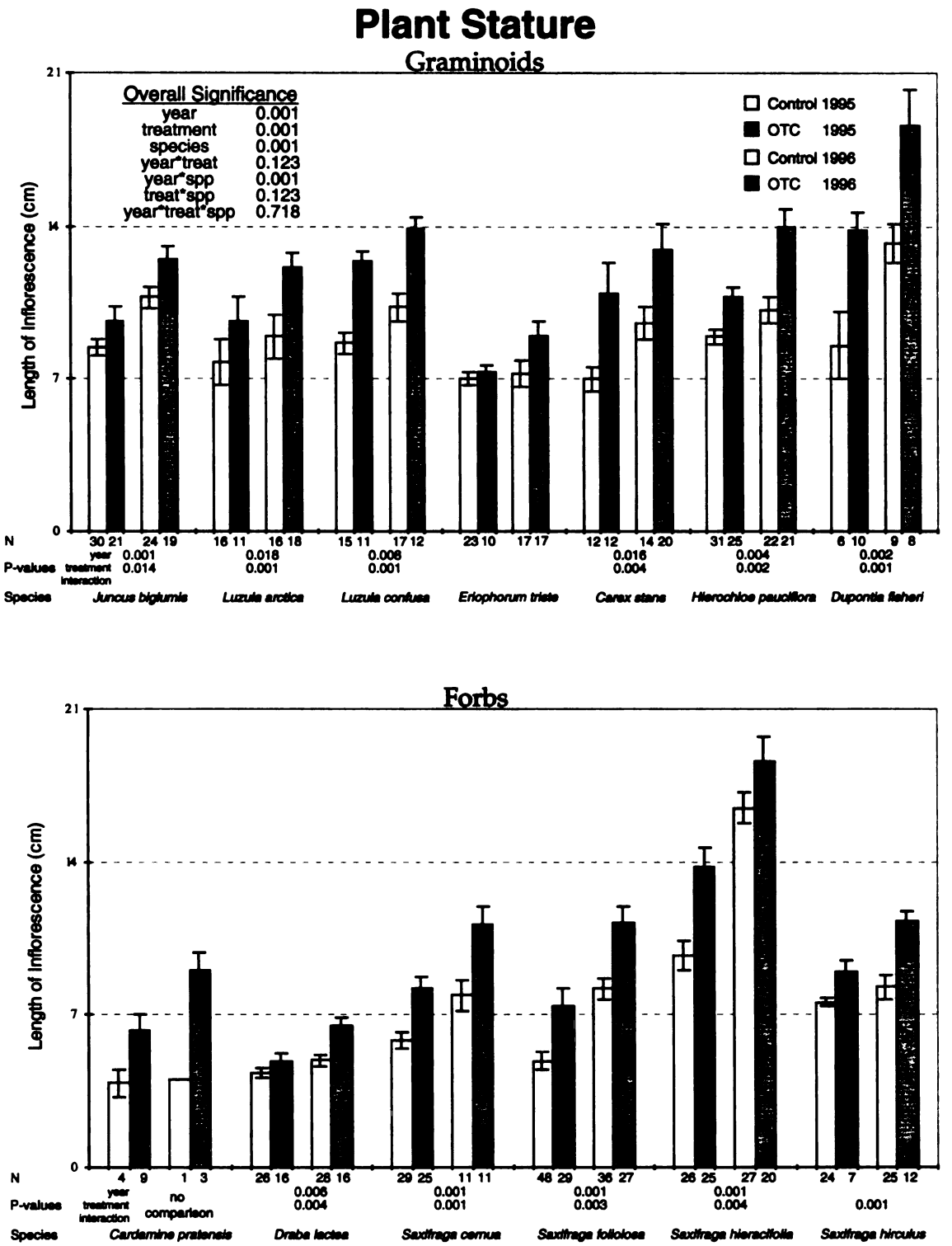


Figure IV-4. End of season measures of the length of inflorescence. Histogram bars represent averages, with standard error of the mean as error bars. P-values of less than 0.05 reported from a two way ANOVA and samples size are given for each species. Overall significance (top left) is reported from a three way ANOVA run on all forbs and graminoids.

IV.2.3 Hypothesis 2c: *The length of leaves will be longer under warmer conditions.*

There was no consistent pattern in leaf length response to chambers or years across species (Figure IV-5). Only one species, *C. pratensis*, significantly responded to chambers and year and the magnitude of response was small. Two species, *S. hieracifolia* and *C. stans*, significantly responded to year and not chambers. The average diameter of rosette was measured on *D. lactea* and *S. foliolosa*; this measure is more reflective of vegetative growth than leaf length. Neither species significantly responded to year or treatment (Figure IV-6). Overall there was no effect of treatment but there was a significant difference between years. The average leaf length was not always longer in the warmer year or in the chambers.

Leaf length does not necessarily reflect true vegetative response because a species may respond by increasing length or number of leaves. For a limited number of species the number of leaves were also measured. The product of leaf length with number of leaves was considered a more instructive measure of vegetative response although not ideal because the length of secondary leaves could be promoted more than the length of the primary leaf. For the product of leaf number with leaf length (vegetative measure) *C. pratensis* and *E. triste* showed both significant response to year and treatment while *S. hieracifolia* and *C. stans* showed a significant response in year only (Figure IV-6). Overall there was a significant difference between both years and treatments. These results show that there is an overall vegetative response to warming but caution must be used because it is based on a small sub-sample of the species of which many significantly responded in leaf length.

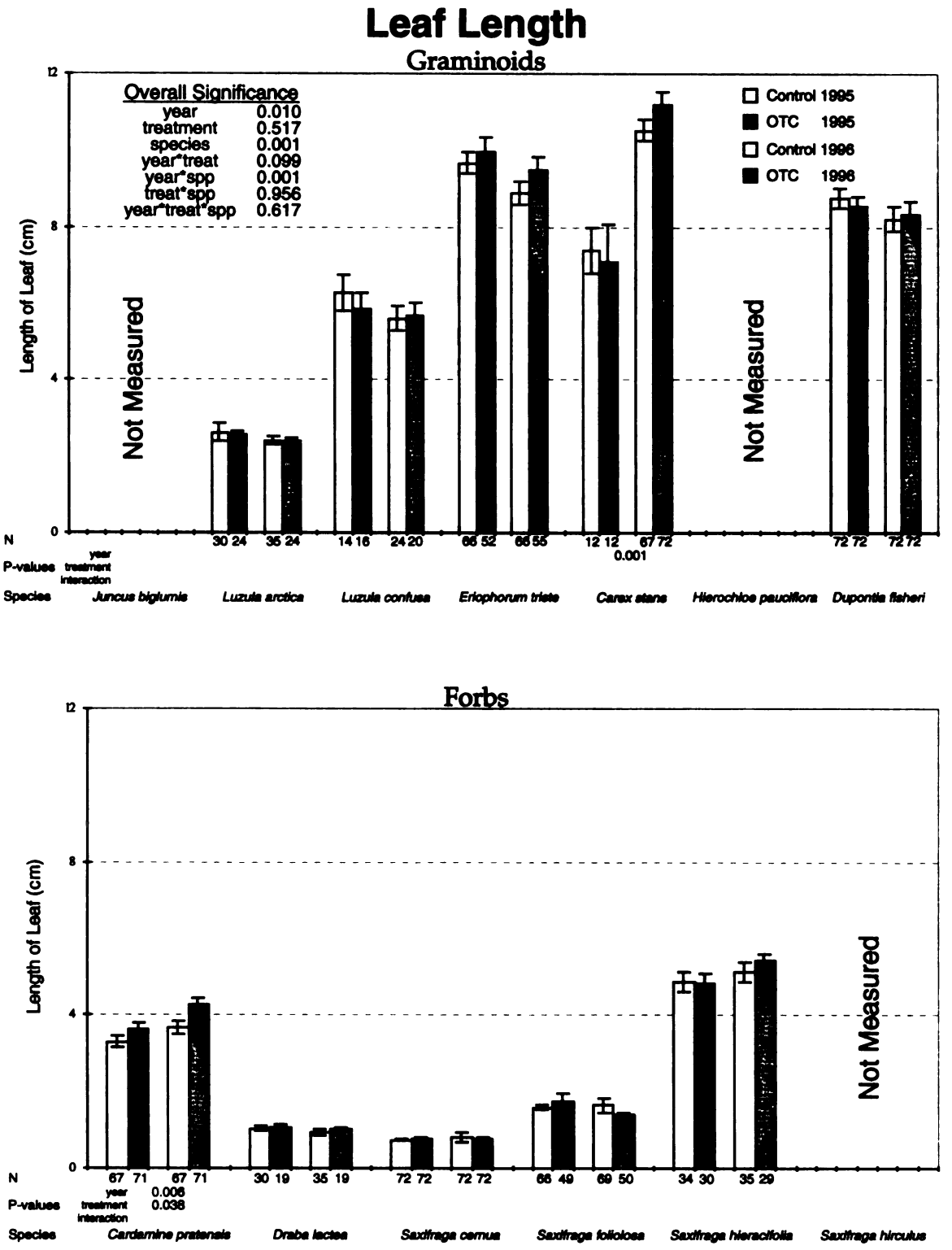


Figure IV-5. End of season measures of the length of longest leaf. For species *D. lactea* and *S. foliolosa* measures are the diameter of rosette. Histogram bars represent averages, with standard error of the mean as error bars. P-values of less than 0.05 reported from a two way ANOVA and samples size are given for each species. Overall significance (top left) is reported from a three way ANOVA run on all forbs and graminoids.

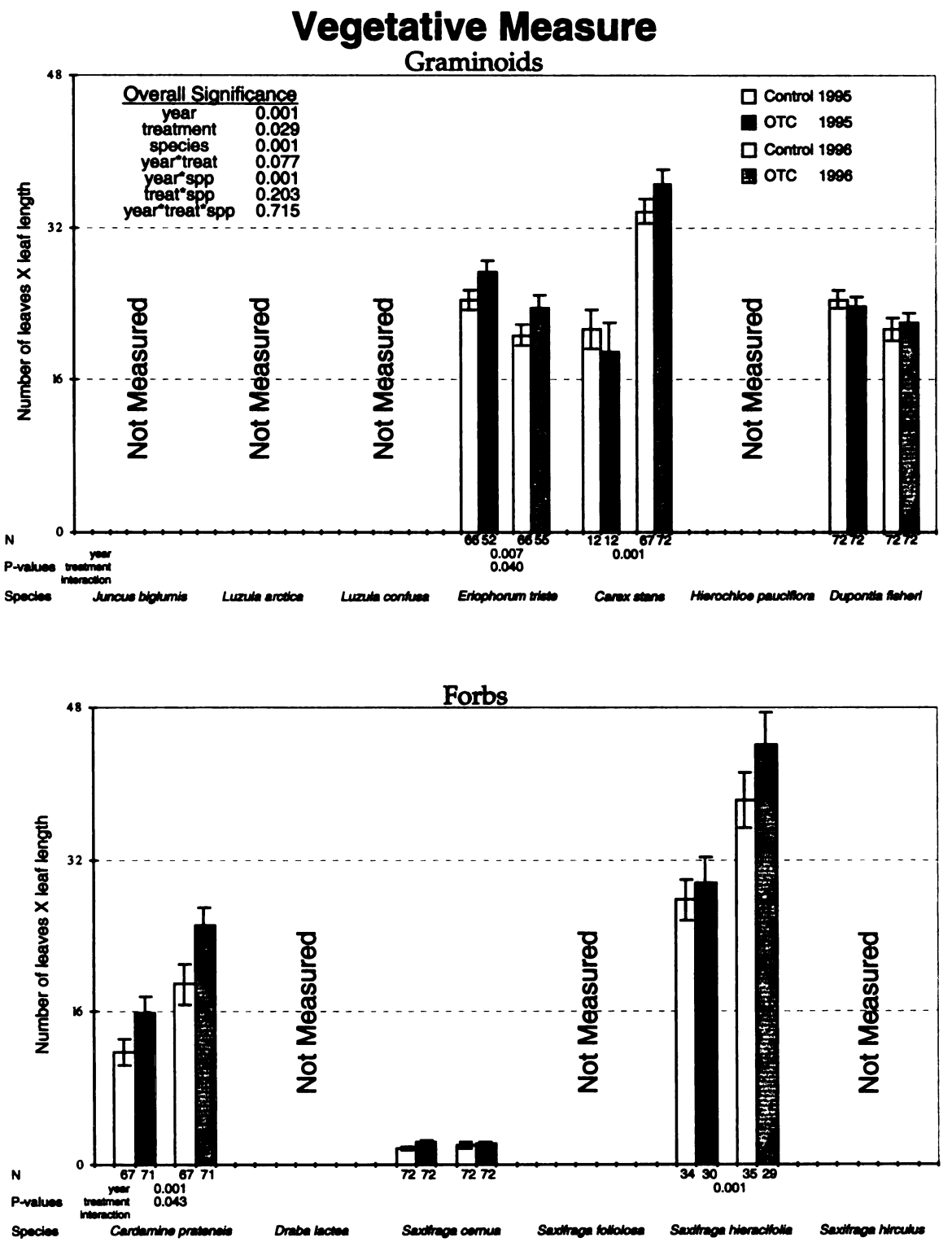


Figure IV-6. End of season measures of vegetative growth (length of the longest leaf multiplied by the number of leaves). Histogram bars represent averages, with standard error of the mean as error bars. P-values of less than 0.05 reported from a two way ANOVA and samples size are given for each species. Overall significance (top left) is reported from a three way ANOVA run on all forbs and graminoids.

IV.3 SPECIES PATTERNS OF RESPONSE

Question: Are there species responses to temperature that can be generalized or do all species respond uniquely?

IV.3.1 Hypothesis 3a: *Short-term plant phenologic response to canopy warming will mirror responses observed in warm years.*

There was a strong similarity of significant response to interannual variability and canopy warming when examining the response of species flowering to degree day accumulations (Figure IV-2). Six species (*J. biglumis, H. pauciflora, D. fisheri, D. lactea, S. hieracifolia,* and *S. hirculus*) responded to year and six (*J. biglumis, E. triste, H. pauciflora, D. fisheri, D. lactea,* and *S. hirculus*) responded to treatment with an over lap of four species that responded to both (Figure IV-2). The average accumulation of degree days until flower opening was always greater in the chambers than in the control of that season. Due to similarities in seasonal degree day accumulations it is instructive to compare the 1995 OTCs with the 1996 controls. From this comparison only two species, *D. lactea* and *J. biglumis,* show significant differences between the two populations (Table IV-2).

IV.3.2 Hypothesis 3b: *Short-term response of plant vigor observed in the chambers will mirror responses of controls observed in warm years.*

The number of flowers within plots showed no consistent response to chambers or interannual variability. No species responded to both interannual variability and

chambers (Figure IV-3). Comparisons made on this variable are not conclusive due to the tremendous variability among plots and the small subset of species measured.

Table IV-2. Statistical significance reported from post factor tests of the population means of the 1995 OTC compared against the 1996 control. The group that responded earlier on average is also presented.

Species	Degree Date of Flowering	earlier average	Number of Flowers /plot	greater average	Length of Inflorescence	greater average	Length of Leaf	greater average	Vegetative Measure	greater average
Cardamine pratensis	-	-	nsd	OTC	-	-	nsd	control	nsd	control
Carex stans	nsd	OTC	nsd	OTC	nsd	OTC	**	control	**	control
Draba lactea	**	control	-	-	nsd	OTC	nsd	OTC	-	-
Dupontia fisheri	nsd	control	**	control	nsd	OTC	nsd	OTC	nsd	OTC
Eriophorum triste	nsd	control	-	-	nsd	OTC	nsd	OTC	nsd	OTC
Hierochloe pauciflora	nsd	control	-	-	nsd	OTC	-	-	-	-
Juncus biglumis	**	control	-	-	nsd	control	-	-	-	-
Luzula arctica	nsd	OTC	-	-	nsd	OTC	nsd	OTC	-	-
Luzula confusa	nsd	control	-	-	**	OTC	nsd	OTC	-	-
Saxifra cernua	-	-	**	control	nsd	OTC	nsd	control	nsd	OTC
Saxifraga foliolosa	-	-	nsd	control	nsd	control	nsd	OTC	-	-
Saxifraga hieracifolia	nsd	control	-	-	**	control	nsd	control	**	control
Saxifraga hirculus	nsd	OTC	nsd	control	nsd	OTC	-	-	-	-

- no comparison possible nsd no statistical difference ** statistical difference

The height of inflorescence responded significantly to both years and chambers. *S. hirculus* was the only species to respond differently to years and treatments. Fortuitously, a comparison of response to interannual variability in temperature and chamber manipulation of temperature can be made due to the fact that similar amount of degree day accumulation from snow melt (TDD*) during the 1995 OTC and 1996 control. For all but two species, *L. confusa* and *S. cernua*, the height of inflorescence was not significantly different between the two populations.

There was no clear pattern of vegetative response to canopy warming or interannual variability; therefore a comparison is of little value. Although, of the four species that did respond to year, two of them, *E. triste* and *C. pratensis*, also responded to

treatment. The two species that only responded to year, *C. stans* and *S. hieracifolia*, may have been responding to climatic features other than temperature. The response in vegetative growth was inconsistent for treatments and years; furthermore, *E. triste* responded positively in chambers and negatively in the warmer year.

Table IV-3. Summary table of significance of year and treatment of all species. All responses were positive in relation to warmth (i.e., earlier flowering; greater numbers of flowers, length of inflorescence, length of leaf, and vegetative measure) except for *E. triste* which had a decreased vegetative response in the warmer year (bold).

	Julian Date of Flowering		Number of Flowers /plot		Length of Inflorescence		Length of Leaf		Vegetative Measure	
Species	Year	Treat	Year	Treat	Year	Treat	Year	Treat	Year	Treat
Cardamine pratensis	-	-	nsd	nsd	-	-	**	**	**	**
Carex stans	**	**	nsd	**	**	**	**	nsd	**	nsd
Draba lactea	**	nsd	-	-	**	**	nsd	nsd	-	-
Dupontia fisheri	**	**	**	nsd	**	**	nsd	nsd	nsd	nsd
Eriophorum triste	**	nsd	-	-	nsd	nsd	nsd	nsd	**	**
Hierochloe pauciflora	**	**	-	**	**	**	-	-	-	-
Juncus biglumis	**	nsd	-	-	**	**	-	-	-	-
Luzula arctica	**	**	-	-	**	**	nsd	nsd	-	-
Luzula confusa	**	**	-	-	**	**	nsd	nsd	-	-
Saxifra cernua	-	-	nsd	nsd	**	**	nsd	nsd	nsd	nsd
Saxifraga foliolosa	-	-	**	nsd	**	**	nsd	nsd	-	-
Saxifraga hieracifolia	**	nsd	-	-	**	**	**	nsd	**	nsd
Saxifraga hirculus	**	**	nsd	nsd	**	nsd	-	-	-	-

- no comparison possible nsd no statistical difference ** statistical difference

IV.3.3 Hypothesis 4: *Plant species will respond individualistically to temperature.*

All species significantly responded to year or treatment for at least one plant measure recorded (Table IV-3). No two species responded similarly to all variables measured. For all variables measured, species were significantly different (Table IV-3). This does not signify that species respond differently but rather for each variable some averages were different across species. For all measures except the degree date of

flowering species responded differently to year as expressed by the species year interaction (Table IV-4). Species only responded significantly different to treatment for the number of flowers per plot. This indicates that the trends of number of flowers per plot in response to chambers were different between species, i.e. some species responded with more flowers and some species responded with fewer flowers.

Table IV-4. Summary table of P-values from overall tests for all measures presented.

Effect	Julian Date of Flowering	Degree Date of Flowering	Number of Flowers per Plot	Length of Inflorescence	Length of Leaf	Vegetative Measure
Species	0.001	0.001	0.001	0.001	0.001	0.001
Year*species	0.003	0.900	0.001	0.001	0.001	0.001
Treat*species	0.174	0.230	0.004	0.123	0.956	0.203

IV.4 Discussion and Conclusions

IV.4.1 Hypothesis 1: Response of Flowering Phenology

The Julian day of flowering was statistically different between years for every species presented (Table IV-2, Figure IV-1). The 1996 field season was much warmer than that of 1995 as shown by the differences in average temperature, snowmelt, and degree day accumulations (see section III.1) and this warmth was likely to have influenced flowering. The date of snow melt and degree day accumulation has been shown to effect onset of flowering in other systems (Leith 1974, Walker *et al.* 1995, Walker 1997). Nearly every species flowered earlier on average within the chambers, and several species, *C. pratensis, S. foliolosa*, and *S. cernua*, only flowered within the

chambers during the cooler field season of 1995 (Figure IV-1, Table IV-2). These findings support the assertion that temperature controls the phenology of flowering.

By expressing the onset of flowering in terms of thawing degree days from snow melt (TDD*) rather than Julian days, a more direct assessment of temperature effects can be determined (Figure IV-2). If the only effects of interannual variability and chambers were a change in temperature, then neither should have a significant effect on flowering when expressed in terms of degree days. The onset of flowering for a species should occur at the same degree day accumulation if temperature is the only controller of flowering. *L. arctica*, *L. confusa*, and *C. stans* flowered at nearly the same TDD*; thus for these species flowering is highly temperature dependent. Other species (such as *D. lactea*, *J. biglumis*, *E. triste*, and *P. arctica*) flowered at a different TDD* for each treatment and year. Most of the species fall somewhere in between the two extremes, implying that flowering is controlled by a combination of temperature and other factors. Because species have their own unique evolutionary histories, they are expected to respond individualistically (Gleason 1926, Sørensen 1941). Species will vary in the plasticity of their response to temperature; by definition it is expected that aperiodic species (Sørensen 1941) will respond more in short-term experiments than periodic species (see section I.2.3-1). Walker (1997) reported similar individuality in response to temperature for the Barrow plant species.

It is presumably ecologically and evolutionarily advantageous for a species to reach the same phenophase at approximately the same Julian date regardless of when snow melt occurred or how many degree days accumulated, given the distinct differences in weather variability throughout the season (Myers & Pitelka 1979). For example, some

species have been shown to modify their rate of phenologic development following increased snow pack accumulations (Johnson 1969, Webber *et al.* 1976). Moreover, plants in Barrow generally enter dormancy or begin senescence in early August although average temperatures remain above freezing well into September (Miller *et al.* 1980). This is seemingly peculiar, especially given the extremely short nature of the growing season, and is most likely an adaptation to overcome the extreme variability and unpredictability of weather in August (Myers & Pitelka 1979). Species may have significantly responded to year and treatment in terms of degree date of flowering because they are in synchrony with environmental and biological factors which are not simulated by the chambers; for example, day length and pollinator activity. For species that responded significantly to treatment or year the magnitude of response was generally less in terms of TDD* than Julian dates. This provides further evidence that temperature is an important determinant of the onset of flowering.

In summary, these data support the notion that the onset of flowering is determined by temperature (Table IV-5). The flowering of some species is more closely linked to temperature than are others, and there is a wide variety of response; however, all species show some correspondence between flowering and temperature.

IV.4.2 Hypothesis 2: Vigor Response

Flower buds are preformed at least one year in advance in nearly all arctic species; therefore, the flowering in a given year is highly dependent on the climate of a previous year or years and a clear response in flowering to a current season's temperature regime is not expected (Sørensen 1941). Furthermore, large variation in flowering

between plots made differences in treatment or year hard to determine. Thus, multi-year bud formation times and heterogeneity in flowering might be invoked to explain the lack of detectable response in the number of individuals flowering within the chambers (Figure IV-3, Table IV-3). In order to evaluate the flowering response without confounded differences in species abundance among plots, the percentage flowering was calculated (Table IV-1). From this data no clear patterns emerge. Changes in flowering percentage and consequently abundance are predicted to occur as a response to chamber canopy warming, but were not found. Subsequent years of this study will be needed to properly test this hypothesis because of multi-year bud formation times. In the short-term there was no generalizable response in the numbers of flowers within a plot to temperature.

Table IV-5. Summary table of the number of species with significant response in their phenology of flower opening (number responding / number examined).

	Year	Treatment	# in common
Julian Day	10 / 10	5 / 10	5
Degree Day	5 / 10	6 / 10	4
# in common	5	3	

* species not included: *S. cernua, C. pratensis & S. foliolosa.*

The highly significant effect of both treatment and year on the height of inflorescence strongly suggests that the plant's stature is directly or indirectly controlled by temperature (Figure IV-4, Table IV-3). This increase in length of inflorescence may be a result of an adaptation to allocate more resources to reproduction during favorable

conditions. Growth and elongation of inflorescence is not predetermined as the actual bud formation is, therefore the inflorescence can directly respond to a current season's climate, although it may be influenced by previous years stored reserves. Increased height may be a result of a balance between short stature to maximize tissue temperatures and the selective advantage of tall stature to raise seeds above the plant canopy to increase potential dispersal distances (Warren Wilson 1957, Savile 1972). The dogma among tundra ecologists is that short stature is an adaptation to maximize tissue temperatures (e.g., Bliss 1988). By maintaining short stature higher metabolic rates can speed fruit development because the fruiting body is closer to the warm ground surface. As a plant increases its height, it rises further above the ground and it is subjected to a harsher environment. Many species have evolved other mechanisms to maintain high tissue temperatures, such as flower shape and dark pigmentation (Bliss 1962, Mølgaard 1982). Within the chambers and in 1996 the temperature at 13cm height was warmer and could have allowed individuals to achieve higher stature while maintaining high tissue temperatures (Table III-1). An example of the importance of both tissue temperature and the height of inflorescence for dispersal is *Dryas* which has evolved to mature fruits near the ground's surface and then expand the pedicle after fruit formation to raise the mature seeds and increase potential dispersal distance. If the inflorescence is above the first covering of snow, seeds may be released above the snow layer and be blown by the wind for hundreds of miles during the long winter and in doing so greatly enhances dispersal distance (Savile 1972).

It has also been proposed that short stature is an adaptation to allocate more energy into seed development that would otherwise be allocated to the inflorescence

(Savile 1972). With increased photosynthate produced under more favorable microclimatic conditions, limited allocation to stature would not be needed.

Regardless of the adaptive reason for the temperature and height of inflorescence relationship there is a clear correspondence for nearly all species in the wet meadow community monitored in Barrow and the dry heath community (Walker 1997). The increase in stature could be the result of cell elongation or increased cell number. This distinction could be very important in relation to nutrient limitations. If the increase were due to cell elongation, then the species would not be as dependent on nutrient availability and a species would be more able to respond under nutrient limitations.

Table IV-6. Summary table of the number of species with significant responses in height of inflorescence and number of flowers (number responding / number examined).

	Year	Treatment	# in common
Inflorescence Height	10 / 12	11 / 12	10
Number of Flowers	3 / 6	2 / 7	0
# in common	3	2	

species not included:
C. pratensis (Inflorescence Height)
D. lactea, S. hieracifolia, J. biglumis, L. arctica, L.. confusa, E. triste, & H. pauciflora (Year)
D. lactea, S. hieracifolia, J. biglumis, L. arctica, L. confusa & E. triste (Treatment)

The response in vegetative growth to temperature was variable. Several species responded to year but not treatment and not all responses were positive (Figures IV-5 & IV-6, Table IV-4). The significant negative effect of year may be related to other climatic parameters such as precipitation. The lack of response may be a result of

predeterminate or periodic growth of species that is not plastic (see section I.2.3-1); furthermore, for some species growth may have been advanced early in the season but not late in the season. This was found in the dry heath community in Barrow (Walker 1997), but was not detectable with end of season measures. Transplants of species into warmer microclimates have shown that the larger size of the more southerly individuals is often genetically predetermined (Shaver *et al.* 1986). The lack of response may also be due to nutrient limitations. In an environment with low nutrients and no light limitation leaf elongation is not necessarily beneficial and it may be more advantageous to allocate additional resources sequestered in a more favorable microclimate to roots or reproduction. The overall significant effects of year and treatment reported from the vegetative measure suggest that the community is responding vegetatively but this is most likely a result of the selection of a subset of positively responding species in the analysis as seen in Table IV-4. It is also possible, although highly unlikely, that the mixing of many different aged individuals has masked a response. The studied species change in size over year as they age, particularly the rosette species; therefore a more reflective measure of response may be the difference between years. This measurement can be used as the experiment continues because the same individuals will be measured in consecutive years.

IV.4.3 Hypothesis 3: Chamber Efficacy

The observation that it takes on average more degree days for the onset of flowering implies that there were unnatural chamber effects and that they do not act as perfect surrogates of interannual temperature variation (Figure IV-2). Although, the

Table IV-7. Summary table of the number of species that showed significant vegetative response (number responding / number examined).

	Year	Treatment	# in common
Leaf Length	2 / 10	1 / 10	1
Vegetative	4 / 6	2 / 6	2
# in common	2	1	

species not included:
S. hirculus, J. biglumis, & H. pauciflora (Leaf Length)
D. lactea, S. foliolosa, S. hirculus, J. biglumis, L. arctica, L. confusa & H. pauciflora (Vegetative)

response of the chambers is very similar to that of interannual variability when examining the number of significant responses (Table IV-2). This could be due to a balance between warmth and developmental time requirements. Degree days do not account for developmental time requirements as directly as Julian days. This lag may also be due to biological cues in the plants as presented in Section IV.4.1. The consistency of higher TDD* accumulations for flowering within chambers suggests that it is not due to plant biology but some attribute of the chambers. Higher TDD* accumulations for phenologic progression was also reported for the dry heath community in Barrow (Walker 1997). The active layer thickness in 1996 suggests that the soil temperatures were warmer and that a larger nutrient pool was available than in 1995. Other studies have shown a strong interaction and even synergism between temperature and nutrient availability (Parsons *et al.* 1994, Chapin *et al.* 1995). Therefore, the warming effect of chambers may be different than natural interannual variability because, in the chambers, the soil temperatures may be uncoupled from air temperatures. This would cause differences in nutrient availability between warming associated with interannual variability or

chambers. This interaction is a very plausible explanation for some of the differences between interannual temperature variation and chamber canopy warming seen in this data set. For example, in the comparison of the 1995 OTC population with that of the 1996 control, whenever there was a significant difference the control population always responded more except for *L. confusa* (Table IV-2).

The increase in daily range of chambers temperatures towards the maxima may alter the quality of warmth in the chambers. This could also explain differences between degree day thresholds for the onset of flowering.

Interannual differences could be attributed to major differences in snow melt as well as other climatic parameters such as precipitation which the chambers are not deliberately designed to modify. Even with the limitations discussed above the overall response in flowering phenology to interannual variation and chambers is similar and likely a result of temperature control. The similarity is confirmed by a comparison of the 1995 OTC and 1996 OTC from which only two species, *D. lactea* and *J. biglumis,* had significant differences in flowering in terms of TDD* (Table IV-2).

Among the vigor characteristics measured there were no results that strongly suggest that the species were not responding similarly to the warmer canopy associated with interannual variability and chambers. In particular, height of inflorescence data suggest the chamber and interannual response are the same; although there does not seem to be a clear correspondence between temperature and vegetative response. The differences in leaf length were only significantly different between years or treatments for two species: *C. stans* which was longer in the warmer year and *C. pratensis* which responded to both year and treatment. *C. pratensis* was the only species to show a

consistent increase in leaf length to temperature enhancement caused by chambers and interannual variability.

The finding that the variability in temperature was greater within the chambers leads to a secondary hypothesis that if the species are responding to temperature the variability of response should also be more variable within the chambers. This hypothesis was tested by examining the residual error of an ANOVA of length of inflorescence performed on both treatments separately. Length of inflorescence was chosen because it was the variable that responded most clearly to temperature. The residual errors were significantly greater within the chambers (6.4 and 11.4 for the control and OTC respectively). The greater variability within the OTCs is also apparent from an examination of the error bars of all the graphs presented. This finding supports the secondary hypothesis that there is greater variability within the chambers.

Species were found to respond similarly to the effects of chambers and interannual variability in temperature. 70% of the time a species responded similarly to both year and treatment for all measures recorded. If a species responded to either year or treatment then 58% of the time the species responded to both. Furthermore, from a comparison of the populations of the 1995 chambers with the 1996 controls 80% of the time there was no statistical difference for all measures presented. The most logical conclusion from these findings is that the species are responding directly or indirectly to temperature. From this it is reasonable to conclude that the short-term response to chambers is a useful forecaster of response to natural interannual variability in temperature. Therefore, it is reasonable to conclude that the long-term plant response to chambers will be a reasonable predictor of species response to global warming, although

caution must be used because chambers are not perfect surrogates of natural variation. Results gained from chambers should be used in conjunction with information on latitudinal and spatial gradient comparisons and plant biology. The combination of these results is necessary to form fundamental understandings of species temperature relations, which can subsequently be used for preliminary forecasts of species response to global warming.

IV.4.4 Hypothesis 4: Individualistic Nature of Species

Plant responses show a clear individualistic response to temperature enhancement. No two species responded similarly to all measures recorded and all species responded significantly to at least one character. Similar results have been reported from many studies and this result is not surprising (Chapin & Shaver 1985b, Oberbauer *et al.* 1986, Walker 1997). Nevertheless the species in the wet meadow responded in a similar fashion in some characters. For example, all but two species, *E. triste* and *S. hirculus,* significantly increased their length of inflorescence during both the warmer field season and within the chambers.

It is clear from an examination of all species that species have different collective adaptive strategies in response to temperature and allocation patterns vary among species. The response of species in vegetative growth and stature will change canopy structure. These changes in addition to others, for example root response, are likely to alter the competitive ability of a species for resources and this will lead to changes in community composition and abundance. Therefore, it is predicted that the long-term response to

warming will be significantly different than the observed short-term response due to species interactions (Chapin *et al.* 1995, Molau 1997).

IV.4.5 Summary and Conclusions

The major conclusions of plant responses to warming in the wet meadow are based on a synthetic average species response. Plants were found to respond similarly to the chambers and interannual variability 70% of the time. These similarities in response show that the chambers are useful simulators of interannual variability in relation to temperature. Nevertheless, the response of flowering phenology in terms of TDD* was that more species responded to treatment than to year, and the average species flowering was always after a greater accumulation of degree days in the OTC's than that season's control. For all other characters the response to year was generally greater; this was likely due to more differences between years than temperature. It is also possible that the air and soil temperatures within the chambers are not strongly coupled as suggested by the active layer data for the two seasons. This notion would provide a plausible explanation for the reduced magnitude of response associated with chamber warming. It is possible that plants in the chambers are more nutrient limited due to cooler soils than when they experience the same level of warmth in a warm year. It is also possible that the quality of warming within chambers is not comparable to naturally warmer conditions because of the increase in daily range of temperatures. Therefore, predictions of species response to temperature must be cautiously made from a combination of results from chambers and warmer years only if they are supported by fundamental biology. Nevertheless, due to the strong similarity in species response to short-term chamber

warming and interannual variability, it is reasonable to conclude that long-term plant response to chambers will be analogous to plant response to global warming.

The onset of flowering for species in the wet meadow responded greatly to temperature, yet the numbers of flowers did not. The likely explanation for no change in the numbers of flowers is that this short-term experiment did not encompass the multi-year bud formation times required for most arctic species. The vegetative responses were found to be variable between species. This is presumably due to the differences in growth strategies (aperiodic and periodic) and likely related to interactions with abiotic and biotic attributes other than temperature including nutrient limitations.

The most consistent plant response was an increase in the length of inflorescence in warmer microclimates for nearly all species. Arctic species allocate larger proportions of energy into sexual reproduction than their temperate homologs, although vegetative reproduction is prevalent and perceived as the norm. For example, flowers of arctic species are generally disproportionately larger than temperate counterparts (Savile 1972) and the allocation of energy to produce seeds is perceived to be higher in arctic species (Chester & Shaver 1982). In fact the effort measured in carbon cost of producing a new tiller of *Eriophorum* by sexual reproduction has been measured to be 10,000 times greater then propagation by vegetative reproduction (Chapin & Shaver 1985a). This suggests that the benefits of sexual reproduction must be great (Bliss 1988). Because of the implied benefits of sexual reproduction and its infrequency it is expected that plants at Barrow will allocate more energy to reproductive characters rather than vegetative characters during more favorable conditions. The consistent increased length of

inflorescence during warmer conditions suggests that plant species are able to capitalize on warm opportunities by allocating more energy to reproduction.

Arctic plants are in a perpetual trade-off to maintain low stature in order to maintain high tissue temperatures for development, photosynthesis, and translocation and to increase stature to raise seeds above the plant canopy in order to enhance competition; for example, dispersal potential and pollination. With increased canopy temperature the balance can be shifted towards taller stature. If this increased stature were due to cell elongation it would be less dependent on nutrient availability and able to respond more than characters that are nutrient demanding. This could become important with predicted changes in nutrient availability, turnover, and demand predicted by warming (Chapin *et al.* 1995, Hobbie 1996).

The combined data show different allocation patterns for various species in the wet meadow. These differences are likely to result in changes in species competitive abilities and ultimately lead to changes in community composition and abundance due to species interactions. Therefore it is predicted that the short-term proximate effects of warming presented in this thesis, which are nearly all positive, will be very different than the long-term ultimate effects of warming. From this the predicted ultimate effect of warming is changes in community composition, structure, and function.

Chapter V

CONCLUDING REMARKS

V.1 RELEVANCE OF THE STUDY IN RELATION TO CLIMATE CHANGE

Arctic summer temperatures are expected to increase by about 4 °C over the next 50 years (Dickinson & Cicerone 1986, Houghton *et al.* 1996) and have recently been rising at the rate of 0.75 °C per decade (Chapman & Walsh 1993). These changes have important feedback implications *via* the effect that vegetation has on atmospheric processes (Shaver & Kummerow 1992, Henderson-Sellars & McGuffie 1995). Yet there is insufficient information on the direction and the rate of change due to direct and indirect responses of the arctic flora, vegetation and soils to warming to make reliable predictions of the future (Chapin 1984, Robinson & Wookey 1997). This project has contributed, and will continue to contribute, to the growing body of knowledge on tundra plant responses to experimental warming (e.g., Chapin *et al.* 1992, Callaghan *et al.* 1995, Henry & Molau 1997, Oechel *et al.* 1997). A large, continuous database is essential for a comprehensive understanding of the system since responses vary widely with latitude and habitat, and long-term responses have generally been found to be different from short-term responses (Chapin *et al.* 1995, Molau 1997). Further, changes in the arctic climate will vary by geographic region (Chapman & Walsh 1993), and will become more variable and extreme (Karl *et al.* 1995, Houghton *et al.* 1996). Tundra plants respond in highly individualistic ways to a range of environmental factors including temperature (Webber 1971, Chapin & Shaver 1985b, Chapin *et al.* 1996). For these reasons, the International Tundra Experiment (ITEX) was established to study both direct and indirect biotic changes to changing climatic factors over a long enough period to encompass

extreme events in order to predict future vegetation and plant patterns over the entire Arctic (see section I.3.2).

The wide taxonomic breath of this study combined with the detailed documentation of chamber performance makes this study the most extensive in ITEX. This study has already contributed a substantial proportion of information to the ITEX network and has a sizable influence on conclusions of the group (Arft *et al.* in prep). It has also made a strong contribution in understanding the chamber dynamics and their weaknesses and strengths as forecasters of species responses to warming.

V.2 Synthesis of the System Response

Nearly every species responded to warming by increasing its stature in the wet meadow. There was no consistent response among species in terms of leaf length. Although there was an overall increase in vegetative response including leaf length and number, this increase was not consistent across species and may be an artifact of the small subset of species used in the analysis. The consistent increases in stature indicate that an investment in current season's reproductive effort is a short-term response to increased temperature. The magnitude and occasionally the direction of response was variable across species for vegetative characters. This indicates that there is a potential for changes in species composition and abundance. Other studies have shown differences between short-term and long-term responses to temperature enhancement (Chapin *et al.* 1995, Molau 1997). These differences have been strongly tied to nutrient availability and

species competition. It is predicted that these differences will also occur in the wet meadow community in Barrow.

The implications of increased stature in almost all species, and increased lengths and numbers of leaves in some dominant species, lends support to the prediction that communities such as the wet meadow in Barrow will respond to warming with an increase in canopy height and leaf area index. This could change the surface energy exchange process that could further influence regional temperature (Chapin *et al.* 1997). A thicker mat of vegetation may also act to insulate the air above the canopy from the soils (Tyrtikov 1959, Shiklomanov 1997). If so, as a result of plant response the soil temperatures may not warm proportionally and may actually cool (Brown & Andrews 1982). This could lead to great nutrient limitations in the soils and shift the selective advantage from aperiodic species that respond greatly to temperature increases to species that are more efficient in nutrient adsorption. The decomposition rates of the system also have very important feedback links to the global system because of the large mass of stored carbon in the tundra soils (Anderson 1991, Hobbie 1996, Waelbroeck *et al.* 1997).

Changes in plant canopy could effect all aspects of the community. With increased canopy height and leaf area there will be more cover for lemmings, and it may be predicted that their numbers will increase. However, animal population cycles are complex and a realistic prediction is not available (Jefferies *et al.* 1992, Chitty 1996). Furthermore, with increased nutrient limitations food quality may decrease (Bryant & Reichardt 1992). Accurate system-level responses to warming are currently unobtainable given the present understanding of the dynamics of biotic responses to warming and

feedback processes. Identifying and understanding similar community level dynamics is a diver of this ongoing research program.

V.3 Implications of the Study

A clear conclusion of this study is that species in the wet meadow community in Barrow respond to temperature increase. Equally important is the similarity in species responses to interannual variability and chamber warming. The chambers were shown to reasonably simulate natural variations in temperature; they increased canopy temperature and caused some soil warming. From a detailed documentation of the chambers over the two field seasons it is clear that the chambers warm the canopy in a predictable manner and at a magnitude that is commensurate with forecasted changes in regional climate. It is also clear that the responses of species are similar to both a warmer canopy caused by chambers or warmer years. This finding suggests that the species are responding, either directly or indirectly, to temperature. However, the chambers may have potential limitations due most notably to potential uncoupling of soil and canopy temperatures. Therefore, conclusions based on chambers must be made in conjunction with other findings. Furthermore, strictly empirical predictions of short-term response to global warming based on chambers will be insufficient and predictions must be based on a combination of response to chambers and natural interannual variation. Long-term response to chambers and interannual variation will not be analogous due to cumulative effects of warming on prior seasons. For the latter predictions a fundamental understanding of process is essential. Only from a combination of processes based on

multiple experimental procedures can realistic predictions of plant response to warming be made.

V.4 Future Work

The results presented in this thesis are part of an ongoing research program on the effects of temperature conducted on a wet meadow and dry heath community in Barrow and at a complementary wet meadow and dry heath community approximately 100 km south in Atqasuk. The study will continue to use the basic experimental design and OTCs. In total there are four primary field sites, each with 24 chambers and 24 control plots. From this large array we are able to examine a large number of species responses and examine how these responses vary among communities and over climatic gradients. In order to make comparisons across diverse taxa, we have been exploring similarities in plant functional type response in order to determine the best predictors of species response.

These manipulations will be continued over many years in order to compare distinctions between short-term response and long-term response. It is hoped that these longitudinal experiments will encounter extreme events that have been shown to often be critical to community composition (Grime 1990, Sparks & Carey 1995). The predictions based on these long-term manipulations will also be compared with historical plots sampled more than twenty years ago. From this we will determine if there have been changes in species composition and if any of the potentially observed changes are

commensurate with predictions based on the observed warming trend of the last twenty years.

In addition, small-scale experiments have been run to determine effects of wind, chamber size, biomass, and revegetation. Many more specifically focused experiments are planned with a particular emphasis on the below ground response to warming. The goal of these experiments will be to determine process and fill the gaps in our understanding of the system's dynamics (Table V-1). For a conceptual diagram of the future research program see Figure V-1.

Table V-1. Three potential small-scale experiments specifically designed to test hypotheses presented within this thesis.

- A detailed documentation of plant tissue temperatures throughout the summer that will establish direct chamber effects on the plants.
- A correlation of soil temperatures at various depths with canopy temperatures to determine if there is buffering of soil temperatures under chambers.
- Cell counts of inflorescences from selected species to determine if increased stature is a result of elongation or increased cell numbers.

The goal of the future work is to integrate and combine our results into a new synthesis that will have application in predicting the response of the Arctic System to global climate change. The project will strive for integration between the paradigms of the individualistic species and of plant functional types. The state of knowledge about arctic plant ecology and physiology, combined with limitations of modeling methods, preclude using the species as a basis for modeling future arctic vegetation. Therefore, modelers seek to predict vegetation change based on a limited number of taxa such as functional groups or plant life forms (Soloman & Shugart 1993, Woodward & Cramer 1996). The future work will examine plant responses to warming within various

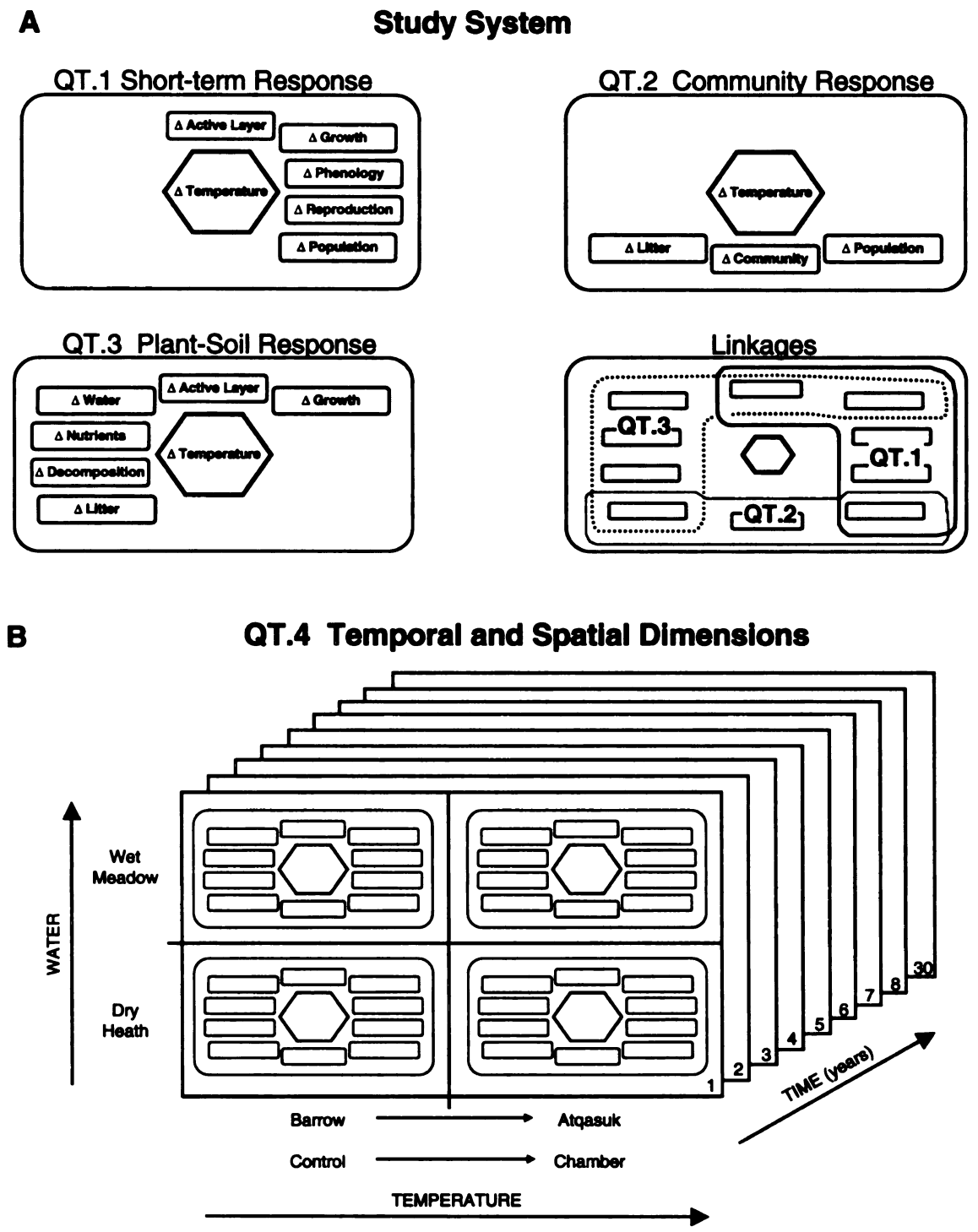


Figure V-1. (A) A conceptual diagram of the tundra plant-soil system components predicted to respond to temperature change and monitored by this ongoing project. The principal domains of the Question Themes (QT) and their regions of overlap indicate important system linkages. (B) The diagrams in A are extended to depict the spatial and temporal dimensions of the project.

traditional species groups based on functional type or evolutionary history and create new "temperature response groups" based on species response to warming (Catovsky 1998). This classification will be created from empirical knowledge of species response to interannual variation and chambers combined with fundamental understandings in biology with emphasis in plant processes and genetics. From this the project will strive towards reasonable predictions of species response to warming in order to provide information to those researchers attempting to realistically model future changes in species composition and abundance due to future climatic warming (e.g., Prentice *et al.* 1992, Woodward & Cramer 1996, Diaz & Cabido 1997).

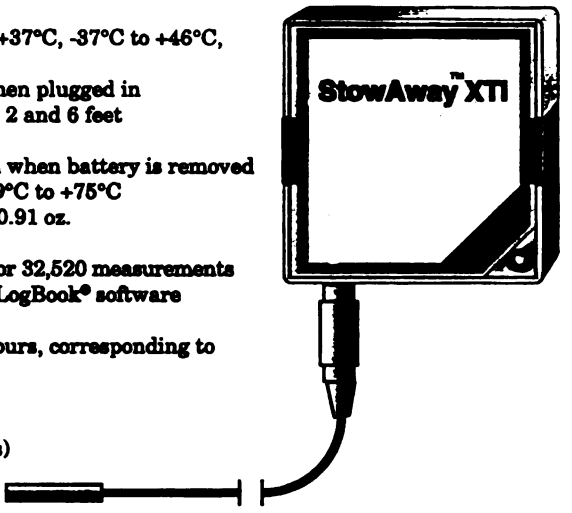
APPENDIX

APPENDIX

Internal temperature logger with optional external probe

StowAway™ XTI

Features



- External probe measures three ranges: -5°C to +37°C, -37°C to +46°C, -39°C to +122°C
- Internal sensor overridden by external sensor when plugged in
- Standard external thermistor probe lengths of 1, 2 and 6 feet
- Two year battery life (user replaceable)
- Nonvolatile EEPROM memory retains data even when battery is removed
- Safe operating temperature range of logger is -39°C to +75°C
- Small size: 1.8" wide x 1.9" tall x 0.6" thick and 0.91 oz.
- Optional submersible case rated to a 400' depth
- 2K, 8K or 32K memory sizes, storing 1800, 7944 or 32,520 measurements
- Start the logger, readout and plot the data with LogBook® software for Windows or Mac
- 42 preselected intervals from 0.5 second to 4.8 hours, corresponding to deployment durations up to two years
- Blinking light confirms operation
- Alarm indication
- Programmable delayed start (up to three months)
- Multiple sampling with minimum, maximum or averaging
- Push button triggered start
- Data exportable to spreadsheet programs (Lotus, Excel, etc.)
- DOS and batch utilities available

Overview

The StowAway™ XTI is a miniature, reliable temperature logger which operates with LogBook® software for PCs or Macs to produce time/temperature data. The StowAway XTI is equipped with an internal sensor for monitoring air temperatures. Using the optional external thermistor cable enables accurate measurements in water or hard-to-reach places.

Individual calibration

Onset Computer Corporation's proprietary test procedures effectively eliminate the resistor and A-D errors, leaving only the thermistor accuracy, quantization error, and a small residual calibration error. Plot A at the right shows the worst case error for the three standard temperature ranges of the StowAway XTI.

Temperature resolution

Plot B shows the temperature resolution of the StowAway XTI for the three temperature ranges. The resolution is the difference between adjacent temperature steps that the logger can record.

Thermal time constant

The thermal time constant (90% response to a step change in temperature) of the external thermistor sensor, used with the StowAway XTI, is less than fifteen seconds when it is in stirred water and less than three minutes in air. The StowAway XTI's internal sensor shows less than a fifteen minute time constant in air.

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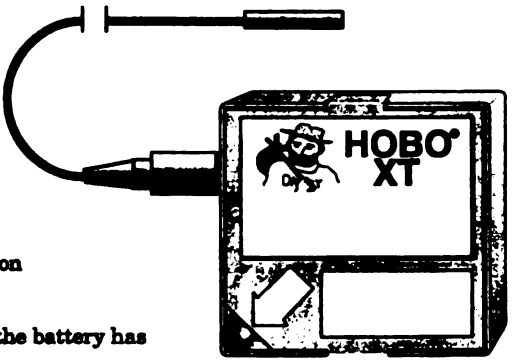
Figure A-1. Specification of the StowAway™ temperature data logger manufactured by Onset Inc.

APPENDIX

Temperature logger with external temperature probe

HOBO® XT



Features

- External probe measures three standard ranges: -5°C to +37°C, -37°C to +46°C, -39°C to +123°C
- Two year battery life (user-replaceable)
- Safe operating temperature range of logger is -39°C to +75°C, non-condensing
- Small size: 1.8" tall x 1.9" wide x 0.6" thick and 0.9 oz.
- External thermistor probe on a flexible cable (ordered seperately)
- Precision thermistor and converters require no calibration
- Standard cable lengths are 1, 2 and 6 feet
- Optional submersible case rated to 400' depth
- Nonvolatile EEPROM memory retains data even when the battery has been removed
- Stores up to 1800 measurements
- 42 preselected intervals from 0.5 second to 4.8 hours, corresponding to deployment durations up to 360 days
- Start the logger, readout and plot the data with BoxCar® or LogBook® software for Windows or Mac
- Blinking light confirms operation
- Data readout in less than 30 seconds
- Data exportable to spreadsheet programs (Lotus, Excel, etc.)

Overview

The HOBO® XT temperature logger utilizes an external thermistor cable which is ideal for recording temperature in hard-to-reach locations. BoxCar® or LogBook® software can start, readout and graph data for Windows or Mac.

Temperature accuracy

The HOBO XT's maximum error is shown in Plot A. This error assumes that all contributing factors to the error are at their maximum values and are aligned so their values add together. These errors include thermistor error, resistor value errors, and quantization error (step errors in the digital representation of the temperature). In a typical logger all errors will be substantially lower.

Temperature resolution

The HOBO XT's resolution (difference between the temperature steps) is shown in Plot B. Note the similarity between the resolution (Plot B) and accuracy (Plot A) for the widest range loggers, where most of the error is due to the quantization error.

Thermal time constant

The thermal time constant (90% response to a step change in temperature) of a HOBO XT's external sensor shows a time constant of less than three minutes in air and less than fifteen seconds in stirred water

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Figure A-2. Specification of the Hobo® temperature data logger manufactured by Onset Inc.

Relative humidity logger

StowAway™ RH

Features

- Rated 5% to 95% RH, non-condensing
- Accuracy ±5% tolerance at room temperature
- Two year battery life (user replaceable)
- Nonvolatile EEPROM memory retains data even when battery is removed
- Memory configurations are 2K, 8K or 32K storing 1800, 7944 or 32,520 measurements
- Safe operating temperature range of electronics is 0°C to 60°C, non-condensing
- Small size: 1.8" tall x 1.9" wide x 0.6" thick and 0.9 oz.
- Start the logger, readout and plot the data with LogBook® software for Windows or Mac
- 42 preselected intervals from 0.5 second to 4.8 hours, corresponding to deployment durations up to 2 years
- Blinking light confirms operation
- Alarm indication
- Programmable delayed start (up to three months)
- Push button triggered start
- Multiple sampling with minimum, maximum or averaging
- Data exportable to spreadsheet programs (Lotus, Excel, etc.)
- DOS and batch utilities available

Overview

The StowAway™ RH is a general purpose, durable, and reusable relative humidity logger. LogBook® software for PCs or Macs makes launching, readout, plotting, and analysis a snap.

Calibration

Each StowAway RH is individually tested at ten relative humidities ranging from less than 10% to greater than 90%. Its calibration is permanently stored in the StowAway RH, ensuring accurate measurements.

Temperature dependence

The StowAway RH sensor has a temperature dependence of 0.22% RH per degree C. A ten degree C excursion from room temperature will add about 2% RH error.

Sensor Specifications

Response time: 2 minutes
Repeatability: less than 2% (constant temperature)
Storage temperature: -40°C to +60°C
Temperature coefficient: 0.22% per °C

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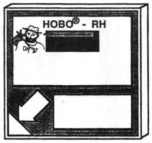
Figure A-3. Specification of the StowAway™ relative humidity data logger manufactured by Onset Inc.

Relative humidity logger

HOBO® RH

Features



- Rated 5% to 95% RH, non-condensing
- Accuracy ±5% tolerance at room temperature
- Two year battery life (user-replaceable)
- Safe operating temperature range of logger is 0°C to 60°C
- Small size: 1.8" tall x 1.9" wide x 0.6" thick and 0.9 oz.
- Nonvolatile EEPROM memory retains data even when the battery has been removed
- Stores up to 1800 measurements
- Start the logger, readout and plot the data with BoxCar® or LogBook® software for Windows or Mac
- 42 preselected intervals from 0.5 second to 4.8 hours, corresponding to deployment durations up to 360 days
- Blinking light confirms operation
- Data readout in less than 30 seconds
- Data exportable to spreadsheet programs (Lotus, Excel, etc.)

Overview

The HOBO® RH is a general purpose, relative humidity logger that is both durable and reusable. Its sensor resists chemical corrosion by chlorine, acetone, pentane, xylene, formaldehyde, ammonia, hospital germicides and freon. The HOBO RH has an operating range of 0°C to 60°C and is designed for a non-condensing environment.

Calibration

Each HOBO RH is individually tested at ten relative humidities ranging from less than 10% to greater than 90%. Its calibrations are permanently stored in the HOBO RH ensuring accurate measurements.

Temperature dependence

The HOBO RH's sensor has a temperature dependence of 0.22% RH per degree C. A ten degree C excursion from room temperature will add about 2% RH error.

Sensor Specifications

Response time: 2 minutes
Repeatability: less than 2% (constant temperature)
Storage temperature: -40°C to +60°C
Temperature coefficient: 0.22% per °C

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Figure A-4. Specification of the Hobo® relative humidity data logger manufactured by Onset Inc.

Light intensity logger

StowAway™ LI

Features

- Calibration ranges from less than 0.001 lumens/square foot to over 1000 lumens/square foot
- Wide spectral response and wide dynamic range
- Two year battery life (user replaceable)
- Nonvolatile EEPROM memory retains data even when battery is removed
- Memory configurations are 2K, 8K or 32K storing 1800, 7944 or 32,520 measurements
- Safe operating temperature range of logger is -40°C to +75°C, non-condensing
- Small size: 1.8" wide x 1.9" tall x 0.6" thick and 0.91 oz.
- Start the logger, readout and plot the data with LogBook® software for Windows or Mac
- 42 preselected intervals from 0.5 second to 4.8 hours, corresponding to deployment durations up to 2 years
- Blinking light confirms operation
- Alarm indication
- Programmable delayed start (up to three months)
- Push button triggered start
- Multiple sampling with minimum, maximum or averaging
- Data exportable to spreadsheet programs (Lotus, Excel, etc.)
- DOS and batch utilities available

Overview

The StowAway™ LI is designed as a durable, reusable, inexpensive, general purpose light intensity logger. Sensitivity ranges from 0.001 lumens/square foot to 1000 lumens/square foot. LogBook® software for PCs or Macs makes launching, readout, plotting and analysis a snap.

Temperature dependence

The StowAway LI is calibrated at room temperature. The logger will read high for temperatures above room temperature and low for temperatures below. The error is approximately a factor of two for every 25°C change. This means it will read a factor of two high at 0°C and a factor of two low at 50°C.

Calibration

The StowAway LI is roughly calibrated for incandescent sources. Full sunlight is about 10,000 lumens/square foot, office lighting is about 50 lumens/square foot, and full moonlight is about 0.03 lumens/square foot. The StowAway LI's range goes from less than 0.001 lumens/square foot to about 1,000 lumens/square foot.

Spectral response

The sensitivity of the StowAway LI's photo sensor extends into the near infrared as shown in Plot A. Although this is useful in many applications, it also means that the logger's responsivity is strongly dependant on the spectral characteristics of the light it is measuring. For example, the logger will read about a factor ten low when reading fluorescent lighting.

Angular dependence

The angular dependence of the logger from 0° to 45° vertical resembles the curve for cosine. After 45° the curve drops off more rapidly.

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Figure A-5. Specification of the StowAway™ light data logger manufactured by Onset Inc.

APPENDIX

Table A-1. Average, maximum, and minimum daily temperature and relative humidity of chambers and controls and climatogical data of the near by NOAA station from snow melt until August 18th for the years 1995 and 1996.

1995

		NOAA						Control						OTC					
	Precip (cm)	Temperature (°C)			Relative Humidity			Temperature (°C)			Relative Humidity			Temperature (°C)			Relative Humidity		
Day		mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min
7-Jul	0	4.8	12.3	2.7	88.3	100	—	4.0	7.1	1.3	—	—	—	6.0	12.3	2.1	—	—	—
8-Jul	1	5.8	17.1	2.0	74.7	95.8	—	9.7	20.1	1.3	—	—	—	10.2	21.2	1.6	—	—	—
9-Jul	0	9.0	17.1	3.1	66.9	100	—	6.8	13.4	3.0	—	—	—	8.8	20.2	3.4	—	—	—
10-Jul	0	3.9	6.0	2.7	82.2	97.9	—	4.6	7.8	2.1	—	—	—	7.1	13.9	2.5	—	—	—
11-Jul	0	2.7	5.0	1.6	81.2	90.4	—	3.1	6.8	1.0	—	—	—	5.6	12.5	1.8	—	—	—
12-Jul	0	2.0	3.2	1.5	86.5	91.0	—	2.4	5.1	0.3	—	—	—	4.9	11.3	1.2	—	—	—
13-Jul	0	1.8	4.6	-0.1	87.6	100	—	4.4	8.8	-0.8	—	—	—	9.2	18.7	-0.1	—	—	—
14-Jul	0	4.1	6.0	1.7	79.9	100	—	5.5	9.6	0.6	—	—	—	9.2	16.8	1.8	—	—	—
15-Jul	1	6.2	10.9	4.4	87.2	98.6	—	7.8	16.3	3.4	—	—	—	10.8	19.1	3.9	—	—	—
16-Jul	0	4.7	8.1	1.6	86.6	100	—	6.0	10.6	1.6	—	—	—	9.3	19.2	2.7	—	—	—
17-Jul	3	8.1	10.9	5.3	93.7	100	—	7.6	10.2	4.3	—	—	—	8.2	10.8	4.6	—	—	—
18-Jul	3	8.9	16.0	4.6	89.1	100	—	9.2	17.6	2.7	—	—	—	9.7	19.1	3.3	—	—	—
19-Jul	6	3.4	10.4	0.1	90.1	100	—	2.7	6.8	-0.2	—	—	—	3.4	8.4	0.0	—	—	—
20-Jul	0	2.9	5.1	1.5	80.2	91.0	—	2.8	5.4	0.8	—	—	—	3.6	7.5	0.9	—	—	—
21-Jul	0	2.0	3.6	0.9	85.9	100	—	2.3	5.3	0.2	—	—	—	4.6	11.5	0.4	—	—	—
22-Jul	0	1.6	3.2	0.3	91.8	100	—	2.2	4.9	-0.2	—	—	—	4.1	9.7	0.0	—	—	—
23-Jul	0	2.4	4.1	1.3	82.0	95.1	—	2.9	7.2	-0.3	—	—	—	5.3	12.3	0.6	—	—	—
24-Jul	0	0.9	3.2	-0.1	88.1	100	—	1.2	4.2	-1.0	—	—	—	3.3	8.4	-0.3	—	—	—
25-Jul	0	0.0	1.7	-1.0	91.8	99.1	—	0.7	3.9	-1.7	—	—	—	3.4	10.0	-1.4	—	—	—
26-Jul	0	-0.4	0.7	-1.8	94.2	99.6	—	0.6	3.5	-2.3	—	—	—	2.8	9.1	-1.8	—	—	—
27-Jul	0	0.9	1.6	0.2	92.0	99.3	—	1.4	4.8	-0.6	—	—	—	5.0	14.8	0.3	—	—	—
28-Jul	0	0.8	2.4	-0.3	91.3	99.8	—	2.3	5.5	-1.2	—	—	—	5.3	12.0	-1.2	—	—	—
29-Jul	0	1.4	2.4	0.4	90.2	97.8	—	1.7	5.0	-0.3	—	—	—	3.5	9.1	-0.2	—	—	—
30-Jul	2	1.4	2.3	0.7	90.6	95.7	—	1.2	2.3	0.1	—	—	—	1.7	3.7	0.1	—	—	—
31-Jul	1	2.5	3.8	1.7	90.7	100	—	3.0	5.7	1.6	—	—	—	4.1	9.5	1.6	—	—	—

— data not available

APPENDIX

Table A-1 (cont'd).

1995 (continued)

		NOAA						Control						OTC					
	Precip (cm)	Temperature (°C)			Relative Humidity			Temperature (°C)			Relative Humidity			Temperature (°C)			Relative Humidity		
Day		mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min
1-Aug	0	4.2	6.5	3.3	92.1	100	—	4.2	8.8	2.4	—	—	—	5.6	14.3	2.6	—	—	—
2-Aug	0	2.7	3.6	2.0	92.7	100	—	2.1	4.8	-0.8	—	—	—	3.8	10.1	-0.2	—	—	—
3-Aug	0	1.1	2.4	-0.2	92.1	100	—	1.7	5.4	-0.9	—	—	—	3.5	11.7	-0.8	—	—	—
4-Aug	0	0.9	2.2	-0.5	96.0	100	—	1.1	4.8	-1.6	—	—	—	3.2	10.2	-1.5	—	—	—
5-Aug	0	1.0	2.4	0.0	93.0	100	—	1.6	4.7	-1.1	—	—	—	3.2	10.5	-0.9	—	—	—
6-Aug	0	2.3	3.4	1.4	93.0	100	—	2.4	4.9	0.5	—	—	—	4.1	9.2	0.5	—	—	—
7-Aug	0	1.3	3.6	0.0	98.3	100	—	1.3	3.9	-0.7	—	—	—	3.5	9.1	-0.6	—	—	—
8-Aug	0	1.8	3.8	0.5	93.4	100	—	3.2	6.5	-0.3	—	—	—	6.1	12.5	-0.4	—	—	—
9-Aug	0	2.7	3.8	1.1	94.7	100	—	3.0	6.8	0.4	—	—	—	4.9	11.9	0.5	—	—	—
10-Aug	0	3.3	5.1	1.3	96.5	100	—	3.7	6.5	0.5	—	—	—	5.4	10.0	0.6	—	—	—
11-Aug	0	3.4	4.9	2.7	97.9	100	—	3.0	5.3	0.9	—	—	—	4.0	7.4	1.3	—	—	—
12-Aug	0	2.6	4.3	1.5	96.9	100	—	3.3	6.8	0.9	—	—	—	4.9	12.2	1.0	—	—	—
13-Aug	0	2.6	4.0	1.5	96.7	100	—	2.6	5.1	0.6	—	—	—	3.9	9.0	0.9	—	—	—
14-Aug	0	2.2	5.5	0.1	93.5	100	—	2.9	8.0	-0.8	—	—	—	3.9	11.5	-0.6	—	—	—
15-Aug	0	3.0	8.1	-0.3	85.0	100	—	4.6	11.6	-1.0	—	—	—	5.7	13.6	-0.7	—	—	—
16-Aug	0	7.7	9.8	5.6	83.5	95.9	—	6.8	11.6	4.2	—	—	—	7.3	13.5	3.9	—	—	—
17-Aug	0	6.2	14.0	2.2	88.4	100	—	6.6	17.0	0.1	—	—	—	8.2	18.5	0.1	—	—	—
18-Aug	1	7.0	10.0	4.6	97.0	100	—	5.3	10.0	0.0	—	—	—	5.6	10.2	0.5	—	—	—
19-Aug		1.0	4.9	-0.5	91.6	100	—	0.1	3.2	-1.9	—	—	—	1.0	6.2	-2.0	—	—	—
20-Aug		0.9	3.6	-0.7	89.5	99.6	—	1.2	5.0	-1.9	—	—	—	1.6	6.6	-1.9	—	—	—
21-Aug		2.0	4.6	0.2	92.0	100	—	2.5	7.7	-5.6	—	—	—	3.8	10.9	-1.8	—	—	—

— data not available

APPENDIX

Table A-1 (cont'd).

1996

		NOAA						Control						OTC					
	Precip (cm)	Temperature (°C)			Relative Humidity			Temperature (°C)			Relative Humidity			Temperature (°C)			Relative Humidity		
Day		mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min
10-Jun	0	-1.1	1.2	-3.1	---	---	---	0.3	2.5	-2.7	---	---	---	3.3	8.4	-2.2	71.7	79.2	61.3
11-Jun	0	-0.9	1.4	-3.2	---	---	---	-0.2	2.5	-2.9	---	---	---	0.9	4.6	-2.7	77.4	85.9	66.8
12-Jun	0	0.6	3.0	-0.5	---	---	---	1.0	3.8	-0.6	---	---	---	2.2	7.6	-0.5	73.7	87.5	60.5
13-Jun	0	1.2	3.4	0.4	97.9	100	---	2.3	4.9	0.3	---	---	---	4.5	11.7	0.3	67.8	81.6	57.9
14-Jun	0	1.5	3.8	0.0	94.7	100	---	2.6	5.8	-0.2	---	---	---	5.5	12.4	0.7	64.6	79.9	58.7
15-Jun	0	1.9	5.4	-0.2	91.9	97.8	---	4.1	7.7	-0.2	---	---	---	6.8	13.6	0.3	64.0	79.0	52.5
16-Jun	0	3.8	13.2	0.7	89.1	97.2	---	6.5	16.0	0.4	84.2	88.8	80.4	8.7	16.9	0.9	75.6	83.8	68.4
17-Jun	0	5.4	8.0	2.5	88.2	98.6	---	6.1	10.2	2.5	78.0	88.3	63.7	6.6	12.6	2.9	66.7	86.0	47.5
18-Jun	0	5.9	11.8	3.0	85.0	99.3	---	9.4	16.5	3.8	62.7	82.6	37.4	11.5	20.9	3.7	50.8	72.3	33.1
19-Jun	0	12.4	22.7	4.5	67.4	92	---	14.4	23.7	3.7	76.5	90.3	63.1	16.2	24.9	6.1	63.6	85.4	46.3
20-Jun	3	8.4	22.8	2.7	76.5	100	---	9.3	16.8	3.2	86.9	92.7	78.8	11.0	20.4	3.6	73.9	87.6	60.8
21-Jun	0	5.5	9.0	3.2	89.7	100	---	5.7	10.1	1.1	89.1	94.0	83.1	7.1	16.4	1.3	74.8	87.1	66.6
22-Jun	0	0.9	5.4	-0.9	95.3	100	---	3.3	11.3	-1.3	85.8	93.5	73.1	5.1	11.5	-1.1	77.2	89.7	68.4
23-Jun	0	5.3	10.8	0.8	85.7	100	---	4.8	9.6	0.1	88.2	94.9	78.7	5.1	9.5	-0.3	76.0	89.7	62.0
24-Jun	1	0.5	2.4	-0.8	88.2	97.3	---	1.8	5.7	-0.8	89.3	94.0	83.1	2.7	8.0	-1.5	74.6	88.7	58.4
25-Jun	0	-0.1	2.0	-1.5	91.9	99.8	---	1.3	4.9	-1.5	89.6	94.9	82.5	3.7	11.0	-1.5	77.6	87.6	67.2
26-Jun	0	0	1.4	-1.1	91.9	99.1	---	1.0	3.7	-0.8	91.4	95.4	86.2	2.2	6.7	-0.6	77.3	89.2	63.2
27-Jun	0	-0.2	1.2	-0.8	95.0	99.5	---	0.9	3.6	-0.9	88.2	93.5	79.8	3.0	8.4	-0.8	68.6	84.3	48.0
28-Jun	0	-0.9	0.3	-2.2	94.0	99.5	---	1.1	5.0	-1.0	82.4	91.1	66.7	5.2	14.7	-0.2	64.5	82.7	41.9
29-Jun	0	-1.4	0.8	-2.7	89.9	96.2	---	1.6	6.9	-2.5	76.2	94.9	62.5	5.4	16.4	-1.6	61.3	86.0	40.2
30-Jun	0	3.6	9.2	0.2	77.1	97.9	---	7.1	13.4	-1.3	89.6	94.9	80.4	10.0	21.5	-0.3	71.1	86.5	45.2
1-Jul	0	2.3	10.5	-1.0	87.3	100	---	2.5	7.1	-0.8	76.0	93.5	56.6	5.7	17.0	-0.3	62.2	87.0	45.8
2-Jul	0	7.7	19.3	0.5	81.4	100	---	11.3	21.4	2.7	85.0	89.8	77.0	12.6	24.2	1.3	69.2	79.9	50.4
3-Jul	0	5.6	8.4	1.8	85.4	97.2	---	7.2	11.8	3.1	90.5	94.4	85.7	9.4	20.8	2.5	77.6	87.0	68.4
4-Jul	0	5.2	7.2	3.2	92.3	97.2	---	5.2	6.8	3.8	82.9	90.7	74.2	6.4	10.9	2.8	68.5	84.9	51.4
5-Jul	0	3.7	5.0	2.6	86.6	93.1	---	5.1	9.0	2.1	89.8	96.2	85.7	7.2	15.6	1.5	74.1	87.6	63.0
6-Jul	2	2.6	4.7	1.2	92.3	100	---	4.2	7.7	1.2	92.8	95.7	87.7	5.5	12.6	-0.2	80.0	88.1	66.1
7-Jul	0	3.4	6.0	2.0	95.8	100	---	4.4	8.3	2.9	93.7	97.5	89.7	5.6	13.4	1.4	82.2	90.3	73.1
8-Jul	1	3.3	7.8	1.6	94.7	100	---	3.9	7.6	0.8	89.7	97.5	80.9	4.1	7.9	-0.2	72.5	90.8	54.4
9-Jul	0	0.6	3.0	-0.8	94.5	100	---	2.0	5.2	-0.5	88.5	94.0	80.4	3.4	10.8	-1.3	70.9	84.9	54.9
10-Jul	0	-0.3	1.4	-1.4	89.6	95.9	---	1.3	5.3	-1.1	89.7	94.4	83.6	3.8	11.4	-0.9	73.7	87.0	63.7
11-Jul	0	-0.4	1.9	-1.5	93.9	99.7	---	1.4	5.0	-1.2	90.1	98.2	75.3	3.6	9.2	-1.0	73.9	91.8	52.0
12-Jul	0	0.8	4.1	-1.2	95.2	100	---	4.6	13.0	-1.0	83.1	91.1	72.5	6.6	18.7	-1.3	67.1	83.8	47.5
13-Jul	8	9	13.7	3.7	83.3	93.8	---	12.0	17.3	5.5	91.1	96.2	85.7	13.7	24.6	4.0	74.4	88.1	57.9
14-Jul	0	8.4	13.3	4.2	93.0	100	---	9.8	15.0	3.8	91.1	96.6	83.6	12.3	24.0	4.2	78.3	91.8	66.7
15-Jul	4	5.2	11.5	1.4	91.9	100	---	4.2	8.0	1.9	96.7	98.2	93.0	5.4	14.1	2.0	90.6	94.8	89.2
16-Jul	3	5.8	8.6	1.5	94.6	99.3	---	6.8	8.3	4.8	97.0	99.0	89.7	6.7	8.0	4.6	90.9	95.3	81.0
17-Jul	1	5.5	6.7	4.6	99.1	100	---	6.6	10.3	4.4	92.6	98.2	83.1	6.6	10.4	4.3	84.2	93.8	73.7
18-Jul	1	7.4	10.7	1.7	88.2	99.3	---	5.9	12.1	0.0	96.6	99.4	89.1	6.5	12.1	1.3	88.9	94.3	81.0

--- data not available

APPENDIX

Table A-1 (cont'd).

1996 (continued)

		NOAA						Control						OTC					
	Precip (cm)	Temperature (°C)			Relative Humidity			Temperature (°C)			Relative Humidity			Temperature (°C)			Relative Humidity		
Day		mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min
19-Jul	2	1.8	9.9	-1.2	98.4	100	—	5.8	14.3	-1.4	96.7	99.0	91.6	6.2	14.2	-0.9	90.4	95.3	87.1
20-Jul	0	6.9	14.2	0.9	93.1	100	—	4.6	10.3	0.1	94.3	98.5	88.1	4.8	10.1	0.5	80.9	94.3	65.0
21-Jul	0	0.9	6.2	-1.1	95.6	100	—	1.8	6.1	-0.6	94.7	98.5	86.1	4.1	10.8	-0.4	85.8	94.8	72.5
22-Jul	0	3.8	8.7	0.0	95.4	100	—	4.5	8.3	0.2	87.9	94.4	79.3	5.0	9.4	0.3	72.4	90.2	53.7
23-Jul	0	0	3.6	-1.6	85.1	95.8	—	2.0	5.8	-1.9	82.0	95.6	64.3	5.0	14.6	-2.0	74.1	89.7	58.4
24-Jul	0	7.4	19.6	1.0	83.9	94.6	—	12.7	20.8	2.7	81.0	94.8	63.1	12.6	21.1	2.6	72.9	90.3	54.3
25-Jul	0	15.5	19.2	10.2	67.1	90.4	—	13.0	20.2	7.5	88.1	98.1	76.5	13.1	20.4	7.4	81.8	93.3	70.7
26-Jul	0	10.7	17.0	7.1	88.2	100	—	12.8	17.2	7.6	85.5	93.9	77.0	12.4	17.1	7.6	76.0	89.2	63.8
27-Jul	0	12.5	17.3	6.2	78.4	94	—	9.9	14.7	3.6	86.7	93.4	79.7	10.5	15.9	3.5	78.5	88.1	70.2
28-Jul	0	4.3	7.4	2.7	81.8	99.3	—	4.2	6.7	2.2	82.3	92.0	69.6	4.4	7.9	2.0	71.5	89.2	53.2
29-Jul	0	3.8	6.0	2.2	77.7	93.8	—	5.4	9.9	1.8	82.2	94.8	70.8	6.9	14.3	1.6	62.3	90.8	42.9
30-Jul	0	3.9	6.6	1.7	82.7	95.8	—	4.5	9.4	-4.4	86.7	95.3	77.0	9.2	19.2	-3.6	73.0	88.1	51.4
31-Jul	0	3	5.9	0.0	82.4	95.1	—	3.9	9.2	-3.1	86.2	96.1	77.5	5.9	16.0	-1.9	71.4	86.5	56.1
1-Aug	0	2.7	7.2	0.2	84.7	97.2	—	4.7	10.0	-1.0	96.8	99.1	94.8	6.4	14.6	-0.8	87.1	91.8	85.4
2-Aug	0	2.8	7.9	0.4	92.4	100	—	2.3	4.8	0.5	94.9	99.1	86.6	2.7	6.2	0.5	81.9	93.3	62.6
3-Aug	0	4.6	10.2	2.3	97.1	100	—	7.1	14.2	2.3	94.1	99.1	87.6	8.3	19.4	2.2	84.5	93.8	72.5
4-Aug	0	6.1	9.2	3.5	93.3	100	—	6.0	10.3	3.5	92.6	98.1	87.1	6.3	11.5	3.4	79.4	93.3	63.2
5-Aug	0	4.3	7.2	2.8	89.7	97.9	—	4.2	7.4	0.9	93.6	98.1	89.0	5.9	12.4	0.9	80.5	93.3	64.9
6-Aug	0	2.6	4.3	1.0	91.5	99.3	—	2.8	7.3	-2.9	93.3	98.5	85.6	4.4	12.3	-2.5	84.0	93.3	75.4
7-Aug	0	2.1	4.6	-0.1	91.0	100	—	3.1	5.8	-0.8	94.7	98.1	86.6	3.5	7.0	-0.8	86.3	93.3	74.8
8-Aug	0	3.7	6.0	2.1	90.9	99.3	—	4.5	8.7	2.2	97.1	99.5	93.8	4.7	9.7	2.2	87.8	93.8	82.2
9-Aug	0	4.4	7.0	1.7	94.9	100	—	3.1	4.8	0.5	91.2	95.1	85.6	3.7	6.0	0.5	81.7	90.8	71.8
10-Aug	0	0.5	2.4	-0.9	86.1	95.1	—	0.8	3.1	-0.8	91.8	95.6	89.0	1.5	5.7	-0.9	82.9	90.8	75.4
11-Aug	0	0.2	2.0	-1.2	85.2	95.3	—	0.9	4.2	-1.5	90.4	94.8	81.9	1.4	6.0	-1.6	76.5	90.2	53.8
12-Aug	0	3	6.5	0.7	87.7	95.8	—	5.3	10.4	1.8	96.2	99.1	91.0	6.8	17.7	1.6	87.6	94.8	81.0
13-Aug	3	4.6	7.4	2.1	92.5	99.3	—	4.8	8.0	1.2	97.1	99.5	90.4	5.0	8.6	1.1	90.9	95.3	86.0
14-Aug	4	6.8	11.2	4.0	92.0	98.6	—	6.8	11.0	1.0	91.1	98.7	79.7	6.7	11.0	1.0	81.7	95.3	66.1
15-Aug	0	2.4	10.8	-0.2	90.1	100	—	1.8	6.1	-0.9	92.1	98.3	84.1	3.3	10.2	-1.1	79.3	91.8	63.8
16-Aug	0	0.5	3.0	-1.0	86.8	96.5	—	2.3	7.3	-1.0	96.1	99.5	91.0	3.7	11.9	-1.2	86.5	96.2	79.3
17-Aug	0	2.5	6.0	-0.6	92.6	100	—	2.0	6.1	-2.1	91.6	98.7	80.8	2.6	6.1	-2.4	78.0	94.3	57.9
18-Aug	0	1.1	4.1	0.2	92.3	99.3	—	3.3	8.6	0.0	98.1	99.5	94.8	5.5	14.7	0.0	89.1	95.3	84.4

— data not available

APPENDIX

Table A-2. Average active layer thickness and standard deviation for the field seasons 1995 and 1996 (N for OTC = 24; N for control = 96).

Day	Active Layer Thickness							
	1995				1996			
	OTC		Control		OTC		Control	
	mean	Std	mean	std	mean	Std	mean	std
10-Jun	---	---	---	---	3.0	0.54	1.5	0.23
13-Jun	---	---	---	---	4.1	0.56	3.0	0.29
14-Jun	---	---	---	---	5.5	0.58	4.3	0.25
15-Jun	---	---	---	---	7.0	0.68	5.6	0.24
16-Jun	---	---	---	---	8.8	0.65	7.6	0.26
17-Jun	---	---	---	---	10.4	0.71	8.8	0.27
18-Jun	---	---	---	---	12.0	0.75	10.9	0.30
19-Jun	---	---	---	---	15.3	0.94	14.1	0.38
20-Jun	---	---	---	---	17.1	0.93	16.1	0.39
21-Jun	---	---	---	---	18.5	0.91	17.6	0.41
23-Jun	---	---	---	---	20.3	0.87	19.3	0.50
24-Jun	---	---	---	---	23.0	1.01	21.6	0.48
25-Jun	2.8	0.25	2.2	0.13	---	---	---	---
26-Jun	2.4	0.24	2.1	0.13	---	---	---	---
27-Jun	2.3	0.22	2.0	0.25	---	---	---	---
28-Jun	2.5	0.22	1.9	0.13	---	---	---	---
29-Jun	3.6	0.23	2.9	0.13	---	---	---	---
30-Jun	4.0	0.23	3.5	0.15	---	---	---	---
1-Jul	5.7	0.22	5.0	0.16	25.2	0.62	23.9	0.51
2-Jul	6.8	0.24	6.2	0.17	---	---	---	---
3-Jul	8.6	0.34	7.8	0.21	---	---	---	---
4-Jul	9.7	0.38	9.3	0.22	---	---	---	---
5-Jul	10.5	0.38	9.9	0.25	---	---	---	---
6-Jul	11.5	0.47	11.4	0.27	---	---	---	---
7-Jul	13.5	0.65	12.6	0.29	---	---	---	---
8-Jul	14.0	0.66	13.9	0.31	---	---	---	---
9-Jul	16.2	0.73	16.4	0.33	---	---	---	---
10-Jul	---	---	---	---	29.9	0.92	29.2	0.61
16-Jul	27.0	0.98	25.0	0.50	---	---	---	---
20-Jul	---	---	---	---	36.2	1.06	36.5	0.64
23-Jul	33.3	1.07	30.7	0.59	---	---	---	---
30-Jul	32.4	1.23	29.8	0.60	44.4	1.93	42.7	0.86

--- no data available

APPENDIX

Table A-2 (cont'd).

Day	Active Layer Thickness							
	1995				1996			
	OTC		Control		OTC		Control	
	mean	Std	mean	std	mean	Std	mean	std
6-Aug	31.8	1.13	29.0	0.55	---	---	---	---
9-Aug	---	---	---	---	45.8	1.27	45.6	0.95
13-Aug	35.3	1.31	33.7	0.67	---	---	---	---
20-Aug	38.0	1.42	35.8	0.74	---	---	---	---
21-Aug	---	---	---	---	50.5	1.54	48.1	0.90
26-Aug	36.8	1.13	35.9	0.72	---	---	---	---

--- no data available

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